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EARLY TERTIARY ADAPISORICIDAE AND ERINACEIDAE (MAMMALIA, INSECTIVORA) OF NORTH AMERICA

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ABSTRACT

The differentiation and relationships among the four earliest known groups of lipotyphlan insectivores concerns the early Tertiary families Adapisoricidae, Erinaceidae, Nyctitheriidae and Geolabididae. The first two families compose the Erinaceomorpha and are considered here. North American adapisoricids comprise *McKennatherium* (*M. ladae*, and an undescribed new species), *Scenopagus* (*S. edenensis*, *S. priscus*, *S. curtidens*), *Ankylodon*, *Talpavus* (*T. nitidus*, *T. duplus*, new species, *Talpavus* sp.), and *Macrocranion* (*M. nitens*). The erinaceids include *Litolestes* (*L. ignotus*, and tentatively, *L. lacunatus* and *L. notissimus*), *Leipsanolestes seigfriedti* and perhaps *Entomolestes grangeri*. *Leptacodon ladae* is here referred to *McKennatherium* and *Entomolestes nitens* to *Macrocranion*. "*Leptacodon*" *jepseni* and "*Diacodon*" *minutus* do not belong in their respective genera. The former may be an adapisoricid. The latter is probably referrable to *Adunator*, a European Paleocene condylarth.

McKennatherium, *Scenopagus*, *Talpavus*, and *Ankylodon* form a lineage of adapisoricids separate from *Macrocranion*, which may have originated in Europe, and which adds to the evidence of a Euramerican fauna during the early Eocene. *Litolestes ignotus* may be central to the radiation of later Tertiary erinaceids, and, along with *Ankylodon*, may have possessed five lower premolars—possibly a primitive character among erinaceomorphs. Adapisoricids and erinaceids share a common origin from a Cretaceous non-paleoryctid-leptictid group of insectivores, which may also have been basal to the radiation of primates, dermopterans, and ungulates.

INTRODUCTION

This study is an elaboration of part of a doctoral dissertation (Krishtalka, 1975) that concerned the systematics and relationships of the oldest known lipotyphlans: the Adapisoricidae, Erinaceidae, Nyctitheriidae, and Geolabididae. That project began as an effort to identify the insectivores from the Powder Wash local fauna, early Bridgerian of Utah, of which the adapisoricids are a mainstay of the discussions in this paper.

The systematics and relationships of the Order Insectivora are among the most perplexing and least understood problems in mammalian evolution. Many workers, among them Gregory (1910), Vandebroek (1961), Van Valen (1967), Thenius (1969), and most recently, Butler (1972) have attempted synthetic reviews of insectivore phylogeny and classification.

Insectivores were first regarded as a distinct group by Illiger (1811) and later divided by Haekel (1866) into the suborders Lipotyphla and Menotyphla. The former comprised shrews, moles, and hedgehogs, or those insectivores that lack an intestinal caecum. The Menotyphla combined tree shrews, elephant shrews, and flying lemurs, or those animals in which a caecum did occur. Although the Menotyphla retain many primitive characters that are lost in the Lipotyphla, they are not a natural group. Flying lemurs and elephant shrews have been relegated to the separate orders Dermoptera (Gill, 1872) and Macroscelidea (Butler, 1956), respectively. The suggested relationships of the tupaiids have swung between primates and insectivores, and Butler (1972) favored an ordinal ranking (Scandentia) for them as well, at least until their affinities are better understood.

Romer (1966) grouped all fossil non-lipotyphlans and some living menotyphlans as the Suborder Proteutheria, essentially a wastebasket taxon. Butler (1972) advocated retention of the Proteutheria, minus the living menotyphlans, as a separate order for the poorly understood fossil non-lipotyphlans, thus limiting the concept of the Insectivora to the Lipotyphla. The resultant Order Lipotyphla would include the living families Erinaceidae, Soricidae, Talpidae, Solenodontidae, Tenrecidae, and Chrysochloridae, and the extinct Adapisoricidae, Nyctitheriidae, Geolabididae, Nesophontidae, Micropternodontidae, Apternodontidae, and Plesiosoricidae. Butler's Order Proteutheria includes the Palaeoryctidae, Lepticitidae, Apatemyidae, Pantolestidae, and Plagiomenidae.

Living lipotyphlans are united by the absence of an intestinal caecum, by a reduced jugal bone, an expanded maxilla in the orbital wall of the skull replacing the palatine, a mobile proboscis served by a series of muscles that affect the form of the skull, a reduced pubic symphysis, absence of the medial internal carotid artery, and an auditory bulla composed mainly of the basispenoid (Butler, 1972). The fossil lipotyphlans are grouped together and with living forms mainly on the basis of dental evidence, although the known cranial remains also support affinities with the Lipotyphla.

Butler (1956, 1972) recognized a fundamental dichotomy among lipotyphlan insectivores—the Erinaceomorpha and Soricomorpha (Saban, 1954)—which he suggested may have originated in the Paleocene. The erinaceomorphs include the Adapisoricidae and the Erinaceidae. In these groups the infraorbital canal is long, the eye is large, and the coronoid process extends posterodorsally. The soricomorphs include the families Geolabididae, Nyctitheriidae, Soricidae, Talpidae, Plesiosoricidae, Dimylidae, Micropternodontidae, Solenodontidae, Nesophontidae and, tentatively, Apternodontidae. These groups possess a short, infraorbital canal, a small eye, and a more nearly vertical coronoid process (Butler, 1956; 1972; personal commun., 1975).

The amount of taxonomic shuffling of nyctitheres, geolabidids, adapisoricids, and erinaceids into various familial, subfamilial, and generic groupings in only the last decade is indicative of the poor understanding of the systematics of these early Tertiary insectivores. Biases of collecting and investigation are moot points in this problem. Most of the early work describing early Tertiary insectivore evolution stems from the study of single local mammalian faunas. Rarely did one investigator have at his disposal all of the pertinent fossil insectivore material from known early Tertiary localities. As a result, taxa were duplicated in the literature and their relationships remained muddled. This problem is magnified when considering relationships between North American and European insectivores (e.g., Russell, et al., 1975). Some recent work, however, has concentrated on the systematics of specific groups like nyctitheriids (Robinson, 1968a), geolabidids (McKenna, 1960b; Lillegraven and McKenna, MS, and European adapisoricids (Russell, et al., 1975).

Remains of insectivores from the following localities were used in this study (see Fig. 1):

Torrejonian:
(1) Gidley Quarry, Lebo Formation, Montana.
(2) Rock Bench Quarry, Polecat Bench Formation, Wyoming.

Tiffanian:
(3) Cedar and Silver Coulee Quarries, Polecat Bench Formation, Wyoming.
(4) Mason Pocket, San Jose Formation, Colorado.
(5) Bear Creek, Fort Union Series, Montana.

Wasatchian:
(6) Four Mile localities, Wasatch Formation, Colorado.
(7) Powder River localities, Wasatch Formation, Wyoming.
(8) Big Horn Basin, Willwood Formation, Wyoming.
(9) Lysite and Lost Cabin, Wind River Formation, Wyoming.
(10) Huerfano localities, Huerfano Formation, Colorado.
(11) Almagre localities, San Jose Formation, New Mexico.

Bridgerian:
(12) Powder Wash, Green River Formation, Utah.
(13) Bridger Basin, Bridger Formation, Wyoming.
(14) East Fork, Tepee Trail Formation, Wyoming.

Uintan:
(15) Myton Pocket, Uinta Formation, Utah.
(16) Badwater localities, ?Tepee Trail Formation, Wyoming.

All measurements are given in millimeters. For those species represented by abundant material, only the observed range in size is presented in the tables, but measurements of each individual specimen appear in the appendices. Although the tooth nomenclature follows Van Valen (1967), Szalay (1969), and Krishtalka (1973), three terms used here in reference to the morphology of P^4_4 in early Tertiary lipotyphlans need further clarification: a premolariform P_4 is characterized by a large, dominant protoconid and an extremely short, usually unicuspid talonid. A small paraconid and metaconid may occur, but they are poorly differentiated from the protoconid.

On a semimolariform P_4 the talonid is much narrower than, but nearly as long as, that on M_1, and usually bears two or three cuspules. The paraconid may be better developed than on a premolariform P_4, but is lower than the metaconid and projects from the anterior part of the base of the protoconid.

A submolariform P_4 is essentially like M_1, except for a narrower talonid and smaller cusps on the trigonid. Characteristically, the paraconid occurs at approximately the same height as the metaconid, and, in this regard, more closely approaches the condition on M_1.

A premolariform P^4 bears only two cusps, a protocone and paracone. A semimolariform P^4 is more like M^1 in possessing a metacone as well.

The recent reclassification of mammals (McKenna, 1975) and its raison d'etre pertains to this and other studies of mammalian phylogeny, especially those which are based almost exclusively on dental remains of fossil mammals and mammalian dental homologies. According to McKenna (1975), the primitive tokothere post-canine dental formula is $dP^1_1P^2_2P^3_3P^4_4dP^5_5M^1_1M^2_2$, in which $dP^5_5M^1_1M^2_2$ have conventionally been referred to as $M^1_1M^2_2M^3_3$, respectively. Recent suggestions of the occurrence of five premolars in *Litolestes*-like erinaceids, *Plagiomene*-like dermopterans (Schwartz and Krishtalka, 1976), and some plesiadapiform-tarsiiform

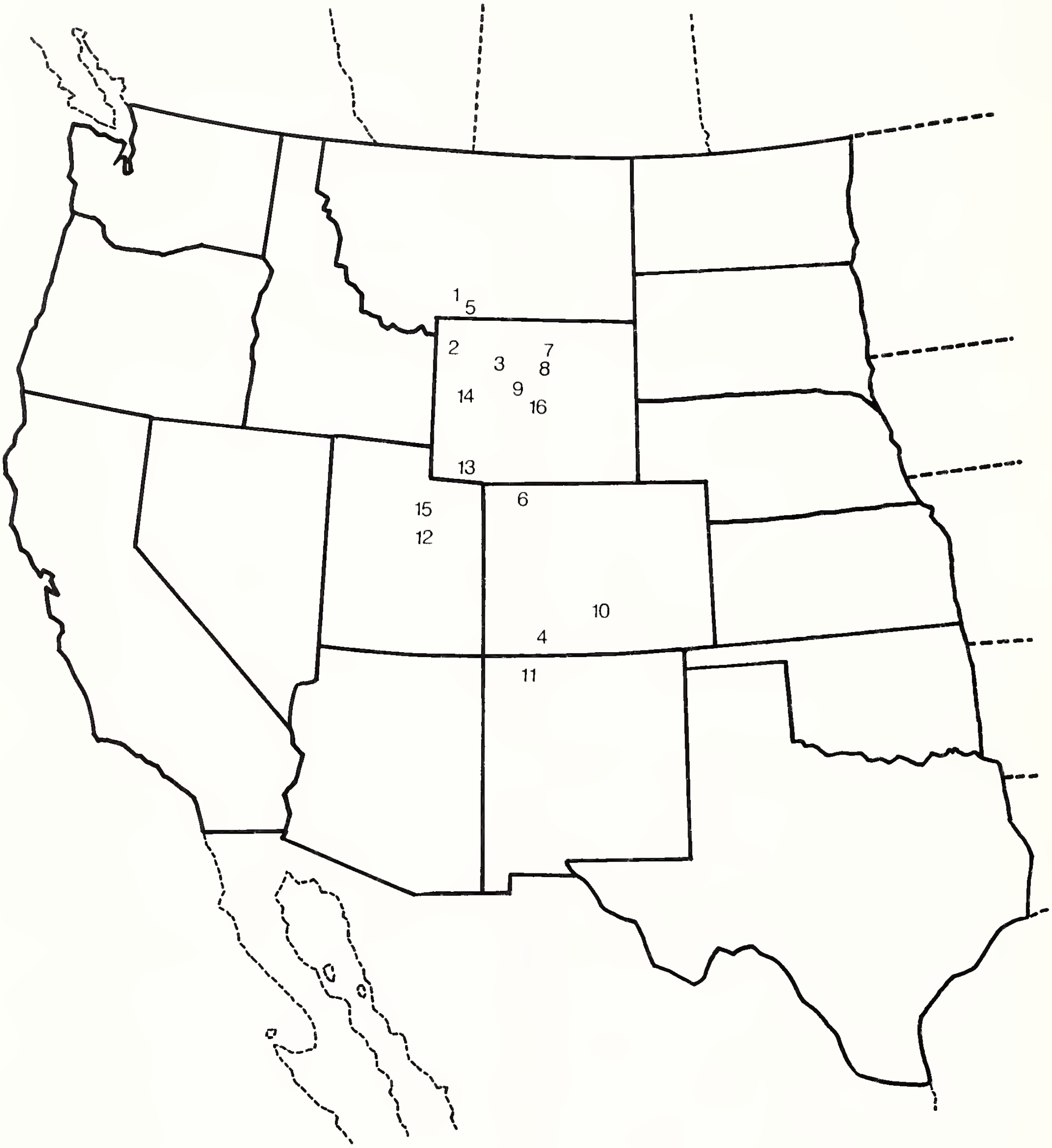


Fig. 1. Geographic location of localities of early Tertiary insectivores described in this paper.

primates (Schwartz and Krishtalka, 1976; Schwartz, in press)—groups that also have three molars—may require an emendation of the dental formula proposed as primitive for tokotheres. A moot point is the homology of the fourth tooth in the lower jaw—the alleged "premolariform canine"—in *Litolestes ignotus* and *Plagiomene multicuspis*. This problem is discussed in detail in Schwartz and Krishtalka (1976) and in the sections in this paper dealing with *Litolestes* and *Ankylodon*.

The use of the conventional P^{1-4}_{1-4} in this paper is a nomenclatorial compromise. Few of the known early Tertiary erinaceomorphs are represented by adequate dental remains necessary to establish dental homologies. *Litolestes* and *Ankylodon* are exceptions, although the deciduous or permanent nature of each of the putative five premolars is uncertain. Also uncertain are the homologies of the premolars in those erinaceomorphs that have four, and the loci involved in the reduction to four premolars from the suggested primitive complement of five.

The abbreviations used in this paper are as follows:

AMNH, American Museum of Natural History
CM, Carnegie Museum of Natural History
PU, Princeton University
TTU, Texas Tech University
UCM, University of Colorado Museum
UCMP, University of California Museum of Paleontology
YPM, Yale Peabody Museum
L, length
W, width
AW, anterior width (width of trigonid)
PW, posterior width (width of talonid)

All photographs are stereoscopic scanning electron micrographs and present occlusal views.

SYSTEMATICS

Family Adapisoricidae (Schlosser, 1887)

Schlosser (1887) erected this family of insectivores to include the European Paleocene genera *Adapisorex* (Lemoine, 1883) and *Adapisoriculus* (Lemoine, 1885). Simpson (1928) added *Entomolestes* and *Leipsanolestes* to this group and relegated *Adapisoriculus* to the marsupials, although the latter has since been identified as a tupaiid (Van Valen, 1965a). Later, Simpson (1945) abandoned the concept of the Adapisoricidae and regarded *Adapisorex* as a leptictid, *Entomolestes* as an erinaceid, and *Leipsanolestes* as a subgenus of *Leptacodon*. Van Valen (1967) revived and broadened the Adapisoricidae to include four subfamilies (Adapisorcinae, Geolabidinae, Nyctitheriinae, Creotarsinae), but acknowledged that many of the generic allocations were tentative. The nyctitheres (Robinson, 1968a) and geolabidines (Butler, 1972) were subsequently removed from the Adapisoricidae and raised to familial rank, an action with which Novacek (in press) and I agree. The Creotarsinae, as Van Valen (1967) acknowledged, is not a natural group.

Of the genera originally assigned by Van Valen to the Adapisoricidae, only the following (in addition to *Ankylodon*) are here recognized as belonging to that family: *McKennatherium* (including *Leptacodon ladae*), *Scenopagus*, *Talpavus*, and *Macrocranion* (including *Entomolestes nitens*, *Aculeodens*, and *Messelina*). *Sespedectes* and *Proterixoides* may also belong here or in the Erinaceidae. Both genera are currently under investigation elsewhere (Novacek, MS). Butler (personal commun., 1975) and I believe that the genus *Adapisorex*, upon which the family is based, is an erinaceid. *Diacodon minutus* may be a condylarth, and is discussed in detail in this paper.

A number of European forms from the Paleocene and Eocene (*Amphilemur*, *Gesneropithex*, *Amphidozotherium*, *Adunator* and *Paschatherium*) that previously had been referred by some authors to the Adapisoricidae have recently been shown to lack affinity with this family of insectivores (Russell, et al., 1975).

McKennatherium Van Valen, 1965b

McKennatherium libitum, named by Van Valen (1965b) as a new genus and species of paromomyid primate, was later shown to be a junior synonym of *Leptacodon ladae* (Szalay, 1968). Van Valen (1967) correctly suggested that *L. ladae* and the genotype of *Leptacodon*, *L. tener*, warranted generic distinction, a point overlooked by Russell, et al. (1975) in their review of North America adapisoricids. Accordingly, *McKennatherium* is a valid genus, although not a primate. Its systematics have never been formalized, nor its relationships described. *M. ladae* is here identified as a primitive Torrejonian adapisoricid, very near the ancestry of *Scenopagus*.

McKennatherium ladae (Simpson, 1935), new combination

(Fig. 2; Table 1)

Leptacodon ladae Simpson, 1935
McKennatherium libitum Van Valen, 1965b.

TYPE: USNM 9640, RP$_4$-M$_3$, Gidley Quarry, Fort Union Formation, Montana.

REFERRED SPECIMENS: AMNH 35954, RP$_3$-M$_3$; and tentatively PU 14774, LP$_3$-M$_1$; PU 14776, RP$_2$, P$_4$, M$_{2\text{-}3}$; PU 14780, LP$_4$-M$_2$; PU 17722, LP$_3$-M$_3$; PU 18500, LP$_3$-M$_3$; PU 19836, RP$_4$-M$_2$.

LOCALITIES: Gidley Quarry, Fort Union Formation, Montana; Rock Bench Quarry Beds, Polecat Bench Formation, Wyoming.

KNOWN DISTRIBUTION: Torrejonian of Montana and Wyoming.

DESCRIPTION: P$_2$ and P$_3$ are double rooted. P$_2$ is essentially a tall, asymmetrical, elongated cusp with a long, concave, posterior slope and a shorter, convex, anterior slope. A minute cuspule occurs at the base of the posterior slope, and a tiny lingual ridge at the base of the anterior one.

P$_3$ is dominated by a high, nearly symmetrical protoconid. A tiny paraconid occurs on the anterior part of the base of the protoconid. The talonid is very short, and consists of a single cuspule that is separated from the posterior face of the trigonid by a labiolingual groove.

P$_4$ of *M. ladae* is semimolariform, with a tall protoconid, a slightly lower metaconid on its lingual face, a low, anterobasal paraconid, and a basined talonid. The talonid is approximately one-half of the width of the trigonid, bears three cusps, and has a straight posterior margin. The paraconid varies in size and in the degree of separation from the anterobasal part of the protoconid.

The lower molars of *M. ladae* are very *Scenopagus*-like, especially resembling *S. curtidens*. Characteristically, the paraconid is compressed to a strong lophid that extends lingually from the protoconid, and is appressed to the anterior face of the metaconid. The paraconid and the metaconid are closer, and the anteroposterior compression of the trigonid is greater on M$_{2\text{-}3}$ than on M$_1$. The protoconid and metaconid are conical, almost bulbous cusps. The talonid is approximately as wide as the trigonid on M$_1$, but extends less labially on M$_{2\text{-}3}$. The hypoconulid is medial, and on M$_3$ projects posteriorly from the elongated talonid. The hypoconid wears flat on M$_{1\text{-}3}$, the entoconid remains high, and the cristid obliqua meets the trigonid labial to the protoconid-metaconid notch. M$_3$ is reduced in *M. ladae* as it is in *S. curtidens* and *S. priscus*.

REMARKS: The molars on the Princeton specimens are slightly wider than on AMNH 35954 and are tentatively referred to *M. ladae*, until a larger sample is available.

M. ladae clearly differs from Paleocene *Leptacodon sensu stricto* (i.e., *L. tener*, *L. packi* and *L. munusculum*) in the lophid-like paraconid and compressed trigonid on the lower molars, the more robust, bulbous cusps, a more external cristid obliqua, and a hypoconid that becomes flat with wear.

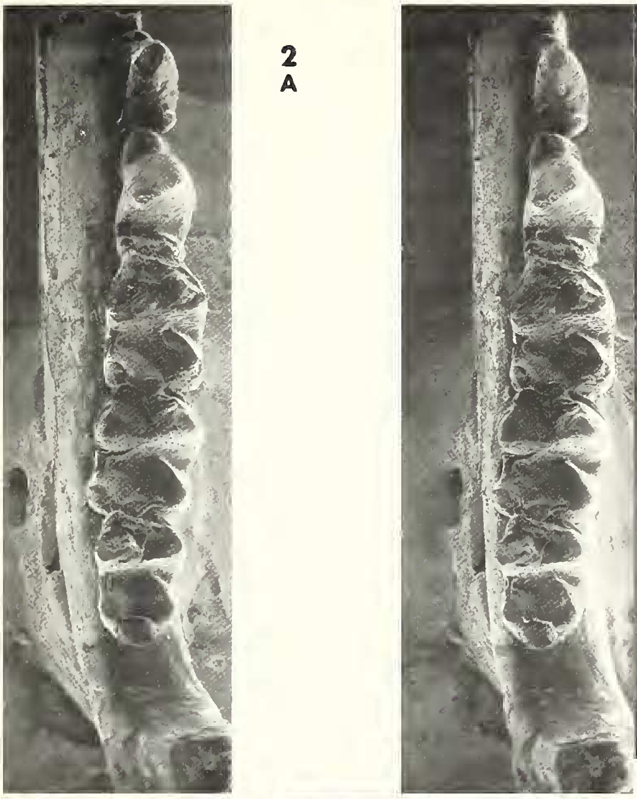
A new and larger species of *McKennatherium*, based on material in the Princeton collection from Rock Bench, Polecat Bench Formation, Wyoming, will be described elsewhere.

The molars of *McKennatherium* are virtually identical in cusp morphology to those of *Scenopagus*. However, P$_4$ in *McKennatherium* is semimolariform, whereas that of *Scenopagus* is premolariform. Premolarization of P$_4$ may be a characteristic trend in lineages of erinaceomorphs (Clemens, 1973), and is implied in the

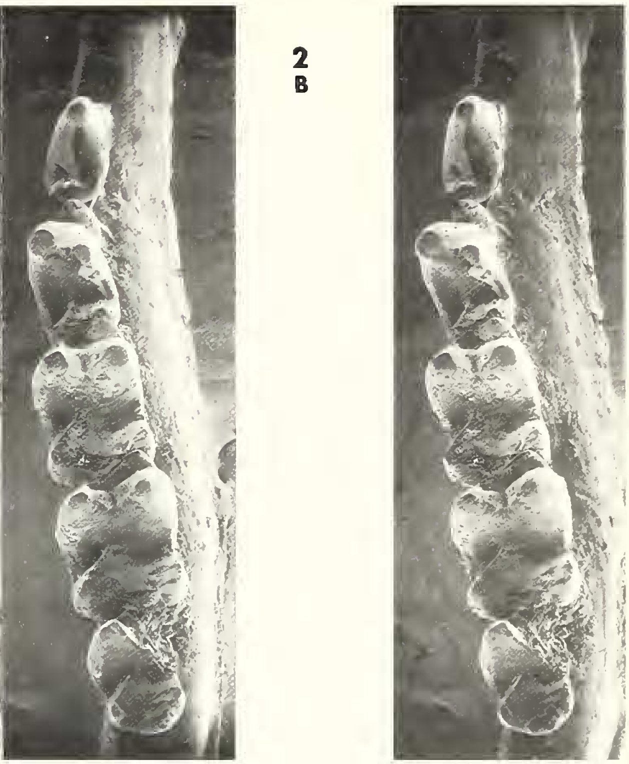
Table 1. Dimensions of lower teeth of *McKennatherium ladae*

	P$_4$		M$_1$			M$_2$			M$_3$		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
AMNH 35954	1.5	0.9	1.6	1.2	1.2	1.5	1.2	1.2	1.6	1.1	0.9
PU 14774	1.8	1.1	1.7	1.4	1.3	—	—	—	—	—	—
PU 14776	1.6	1.0	—	—	—	1.7	1.3	1.4	1.7	1.3	1.0
PU 14780	1.6	1.1	1.7	1.3	1.3	1.6	—	1.4	—	—	—
PU 17722	1.6	1.0	1.7	1.3	1.3	1.7	1.4	1.3	1.6	—	0.9
PU 18500	1.7	1.1	1.7	1.4	1.4	1.7	1.5	1.4	1.8	1.3	1.0
PU 19386	1.6	1.0	1.7	1.2	1.2	1.8	1.4	1.3	—	—	—
Mean	1.63	1.03	1.68	1.30	1.28	1.67	1.36	1.33	1.68	1.23	0.95

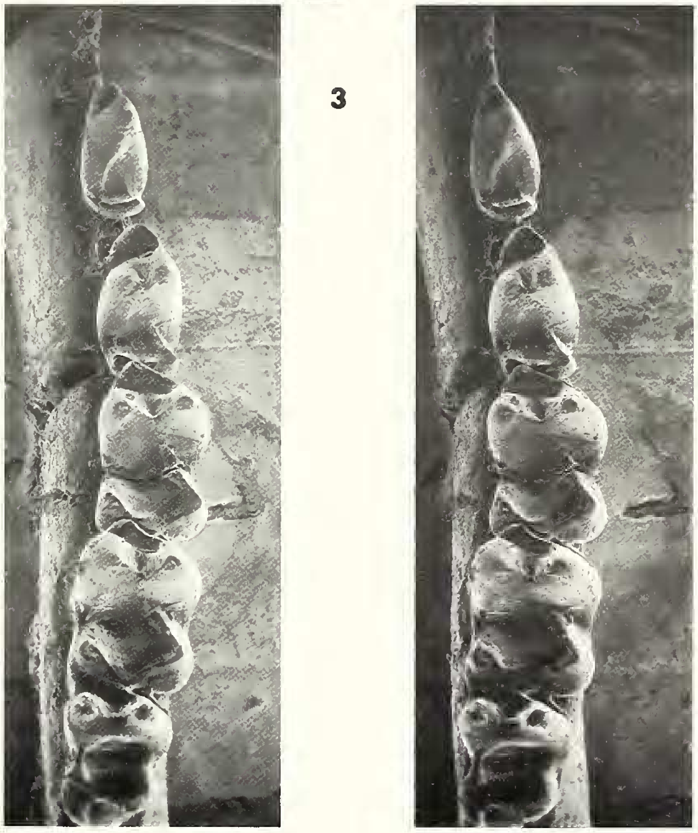
Fig. 2. *McKennatherium ladae*. (A) AMNH 35954, RP$_3$-M$_3$, Fort Union Formation, Montana: approx. X 10; (B) PU 17722, LP$_3$-M$_3$, ▶ Polecat Bench Formation, Wyoming, approx. X 12. Fig. 3. "*Diacodon*" *minutus*, PU 19395, RP$_3$-M$_3$, Polecat Bench Formation, Wyoming, approx. X 12.



2
A



2
B



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transition from *McKennatherium* to *Scenopagus*. *McKennatherium* appears to be a primitive Torrejonian representative of an adapisoricid lineage that included the species of the Eocene *Scenopagus* and *Ankylodon*.

"*Diacodon*" *minutus* Jepsen, 1930
(Fig. 3)

The generic and familial status of this species is in doubt, having been referred to the leptictids *Diacodon* (Jepsen, 1930) and *Palaeictops* (Gazin, 1956), and to *Leptacodon*, ?Metacodontidae (McKenna, 1960a). Some investigators (C. B. Wood; K. Rigby, personal commun., 1974, 1975) have noted that "*D.*" *minutus* is similar in some respects to hyopsodontid condylarths.

The type of "*D.*" *minutus* was recovered from the Silver Coulee Beds, Polecat Bench Formation, late Tiffanian, of Wyoming. Additional material referrable to this species is known only from the type locality and the older, early Tiffanian, Cedar Quarry beds of the Polecat Bench Formation.

"*Diacodon*" *minutus* is not a species of the leptictids *Diacodon* or *Palaeictops* or of the nyctitheriid *Leptacodon*. Its lower dentition is virtually identical to the type of *Adunator lehmanni* (Wa 368) from the Tiffanian Walbeck fauna of Europe (Russell, 1964), an observation also noted by Russell and C. B. Wood (personal commun., 1975). However, the known parts of the upper dentition of "*D.*" *minutus* are not quite as similar to those of *Adunator*. Relative to *Adunator*, M^{1-2} of "*D.*" *minutus* are more transverse, with taller, more nearly conical cusps, a deeper labial emargination, and a weaker hypocone. A problem inherent in this comparison is the degree of certainty of association of the upper and lower dentitions in each of the two taxa.

In the original description of "*D.*" *minutus*, Jepsen (1930) stated that the remains of the upper and lower dentitions were associated, inasmuch as they were found inches apart. The association of upper and lower teeth of *Adunator* is less convincing (Russell, 1964). Although Russell (1964; *in* Russell, et al., 1975) originally identified *Adunator* as a leptictid, his recent restudy of the genus indicates that its affinities lie more with the condylarths (C. B. Wood, personal commun., 1975)—a conclusion I reached independently concerning "*D.*" *minutus* (Krishtalka, 1975).

The lower molars of *Adunator*-"*D.*" *minutus* are also similar to those of the adapisoricid *McKennatherium ladae*, except for a number of moot features: the talonid on M_{1-2} is slightly elongate, and M_2 is larger than M_1. The paraconid on M_2 is extremely compressed and is merged with the anterior face of the metaconid. The metaconid, in turn, is greatly expanded anteriorly, in lingual view, so that it is much larger and more bulbous than the protoconid. These exceptions to adapisoricid affinities in the lower molars of *Adunator*-"*D.*" *minutus* are features associated with some Tiffanian hyopsodontid condylarths like *Haplaletes*. However, the molars in *Haplaletes* have much lower crowns and are more nearly bunodont and robust.

P_4 in *Adunator*-"*D.*" *minutus* is submolariform, with a well-developed paraconid as high as the metaconid. As such, P_4 differs from the semimolariform P_4 of *McKennatherium*, and is closer to P_4 of *Haplaletes*. Similarly, the paraconid is strong on P_3 in "*D.*" *minutus*, weaker in *Haplaletes*, and absent from P_3 of *McKennatherium*. On the basis of the lower dentition alone, *Adunator*-"*D.*" *minutus* appear to be adapisoricid-like hyopsodontids, and may be congeneric.

Scenopagus McKenna and Simpson, 1959

After McKenna and Simpson (1959) described *Scenopagus mcgrewi* as a new erinaceid insectivore, McGrew (1959) and McKenna (1960a) noted that a number of the species included by Matthew (1909) in *Nyctitherium* warranted generic separation and bore specific resemblance to *Talpavus* and *Scenopagus*. Following these suggestions, Robinson (1966, 1968a) referred *Nyctitherium priscum* and *N. curtidens* to *Scenopagus priscus*, and arrangement accepted by Russell, et al. (1975). Earlier, Robinson (*in* McKenna, et al., 1962) had advocated the synonymy of the leptictid *Diacodon edenensis* (McGrew, 1959) with *Scenopagus mcgrewi* and combined the two as *S. edenensis*. Thereafter, *Scenopagus* material recovered from Bridgerian and Late Wasatchian localities (Robinson, 1966; McGrew and Sullivan, 1970; West, 1973) was referred either to the larger *S. edenensis* or to the smaller *S. priscus*. Examination of the sample of *Scenopagus* from Powder Wash and the Bridger Formation now allows clearer definition of the species of *Scenopagus* and the ancestry of the late Eocene and Oligocene *Ankylodon*.

Scenopagus edenensis (McGrew, 1959)
(Fig. 4; Tables 2, 3)

TYPE: AMNH 55685, P_4-M_3, Tabernacle Butte, Bridger Formation (Upper), Wyoming.

REFERRED SPECIMENS: P^4: TTU-P- 7145, 7146, 7147, 7148, 7149. M^1: TTU-P- 7150, 7151, 7152, 7153, 7154, 7155, 7156, 7157, 7158, 7159, 7175. M^2: TTU-P- 7170, 7171, 7172, 7173, 7174, 7176, 7177, 7178, 7179, 7167, 7168, 7169. M^3: TTU-P- 7190, 7191, 8232, 8233, 8234. DP^4: TTU-P- 8235, 8236, 8237, 8238, 8239, 8240, 8241, 8242, 8243. M_1: TTU-P- 7161, 7162, 7163, 7164, 7165, 7166. M_2: TTU-P- 7180, 7181, 7182, 7183, 7184, 7185, 7186, 7187. M_3: TTU-P- 7188, 7189. CM 13739, LP_4-M_1; CM 13732, RM_{2-3}; CM 13734, RP_2M_1; CM 13728, RM_{2-3}; CM 6449, RM_{1-3}; CM 13731, RM_1; CM 13740, RM_2; CM 6444, LP_3-M_1; CM 6441, RP_4, M_1; CM 17318, RP_3-M_1; CM 13737, LP_4; CM 13730, RP_2, P_4-M_2; CM 13729, LM_{1-2}; CM 13735, LP_4; CM 6485, RP_2-M_2; CM 13733, LM_2; CM 13736, M_3; CM 13738, RP_4; CM 6443, RM_{2-3}; CM 17317, RM_{2-3}; CM 13741, P^4-M^2; CM 6433, P^4-M^2; YPM 13612, LM_3; YPM 16910, RM_{2-3}; YPM 14934, LM_{1-2}; YPM 14932, RM_2; YPM 16911, RM^1; AMNH 11428, RM_{1-2}; TTU-P- 5571, RM_{1-2}; TTU-P- 5572, LM_{2-3}.

LOCALITIES: Powder Wash, Green River Formation, Utah; Dry Creek, Lone Tree, Henry's Fork, Phil Mass Ranch, Bridger Formation (Upper), Wyoming; Grizzly Buttes, Black's Fork, Bridger Formation (Lower), Wyoming; Lost Cabin, Wind River Formation, Wyoming; locality III, Huerfano Formation, Colorado.

KNOWN DISTRIBUTION: Bridgerian, Wyoming; late Wasatchian, Wyoming and Colorado.

DESCRIPTION: Much of the lower antemolar dentition is preserved on CM 13730, CM 6485, CM 17318, and CM 13734, partial mandibles from Powder Wash. P_1 and P_2 are single-rooted, essentially unicuspid teeth, with an incipient paraconid on the antero-lingual face of the protoconid, and a tiny cingular heel. P_3 is double-rooted and lacks a metaconid. The paraconid is not a distinct cusp, but a flange projecting from the anterolingual part of the base of the large rounded protoconid. A paracristid extends from the apex of the protoconid to the paraconid flange. The talonid, which is extremely short, is developed as a weak labiolingual ridge separated by a narrow groove from the posterior wall of the trigonid. A tiny cuspule (?hypoconid) occurs on the talonid ridge and is linked to the trigonid by a faint crest (?cristid obliqua).

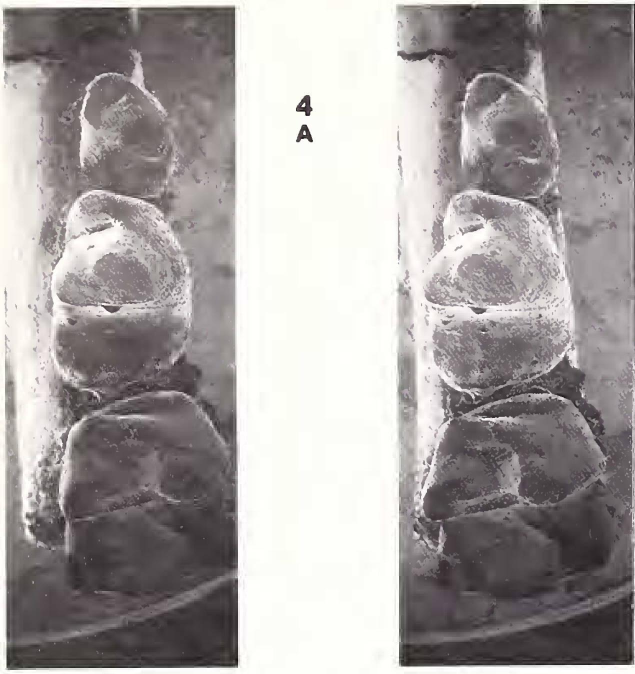
P_4 is premolariform, with a prominent trigonid and a shorter, unicuspid talonid. The base of the talonid is wider than the trigonid, but the dorsal width of the talonid, from the cristid obliqua to the internal edge of the crown, spans only the lingual one-third of P_4. The protoconid is the major cusp of the trigonid. A small, conical paraconid arises from the anterolingual part of the base of the protoconid. The two cusps are linked by a paracristid, and share a continuous, curving, labial-anterolabial face, but are demarcated lingually by a shallow, vertical notch. The metaconid, on the lingual face of the protoconid, is approximately one-half the height of the latter and slightly higher than the paraconid. The cristid obliqua is short and extends directly posteriorly from the trigonid to a small hypoconid. The entocristid slopes downward, lingually and forward from the hypoconid to the posterolingual part of the base of the trigonid, and completes enclosure of the shallow-basined talonid. Characteristically, a deep furrow occurs on the external wall of the talonid from the cristid obliqua to the base of the crown.

The lower molars of *S. edenensis* lean lingually and are essentially rectangular in occlusal outline, with a slight constriction between the talonid and trigonid. The trigonid, approximately one-third higher than the talonid, is wider than the talonid on M_{2-3} but is as wide as, or narrower than, the talonid on M_1. M_3 is unreduced, has an elongate talonid, and is longer than M_1 or M_2. The protoconid and metaconid are high, rounded cusps, barely compressed anteroposteriorly, with the metaconid slightly larger and taller. The paraconid is not a distinct cusp. Rather, it is compressed into a strong, broad paracristid that runs lingually from the anterior part of the base of the protoconid and ends anterior to and merged with the base of the metaconid. Characteristically, in lingual view the notch between the paracristid and metaconid is much higher than the talonid notch at the junction of the entocristid and base of the metaconid. In *Macrocranion* (=*Entomolestes nitens*) the paracristid notch is only slightly higher than, or at the same level as, the talonid notch. The trigonid on M_1 of *S. edenensis* is less compressed anteroposteriorly than on M_{2-3}, and is more nearly triangular.

The talonid basin on M_{1-3} is deep, the hypoflexid shallow. The cristid obliqua is strong and meets the trigonid wall labial to the ventral notch between the protoconid and metaconid. The entoconid is the highest and sharpest of the talonid cusps and is rarely worn, whereas the hypoconid is lower and more nearly rounded, becoming flat with wear. The hypoconulid, smaller than, and distinct from, the entoconid and hypoconid, occurs only slightly lingual to the midline, and on M_3, projects posterodorsally.

Two mental foramina occur in *S. edenensis:* one below P_4 and the other below the anterior root of P_3.

P^3 through M^2 of *S. edenensis* have been adequately described elsewhere (McKenna and Simpson, 1959). Isolated M^3s identified from Powder Wash are narrower and shorter than M^2, possess a strong, flaring parastylar salient, and lack a hypocone. As on M^{1-2}, the protocone on M^3 is compressed anteroposteriorly, and the conules are evident, but fairly small. The buccal edge of the crown, oriented anterolabially, is defined by a weak ectocingulum, and, unlike M^{1-2}, is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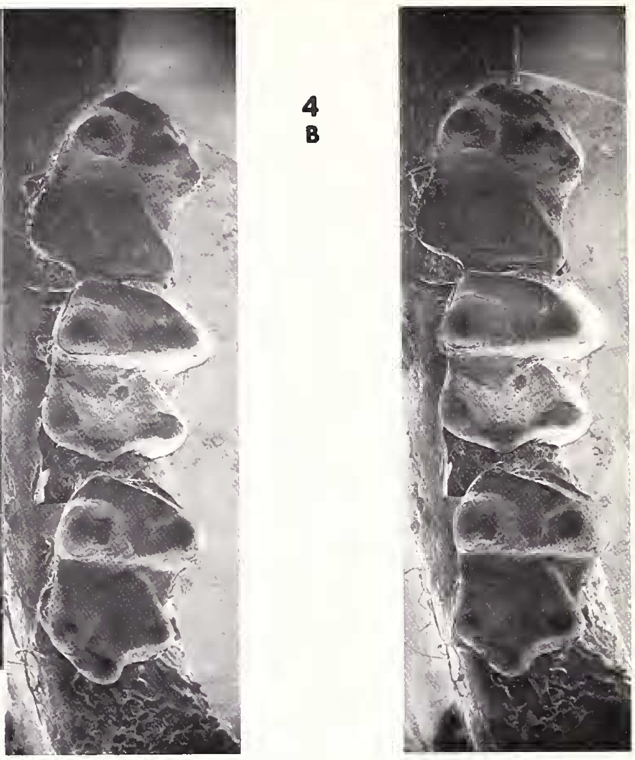
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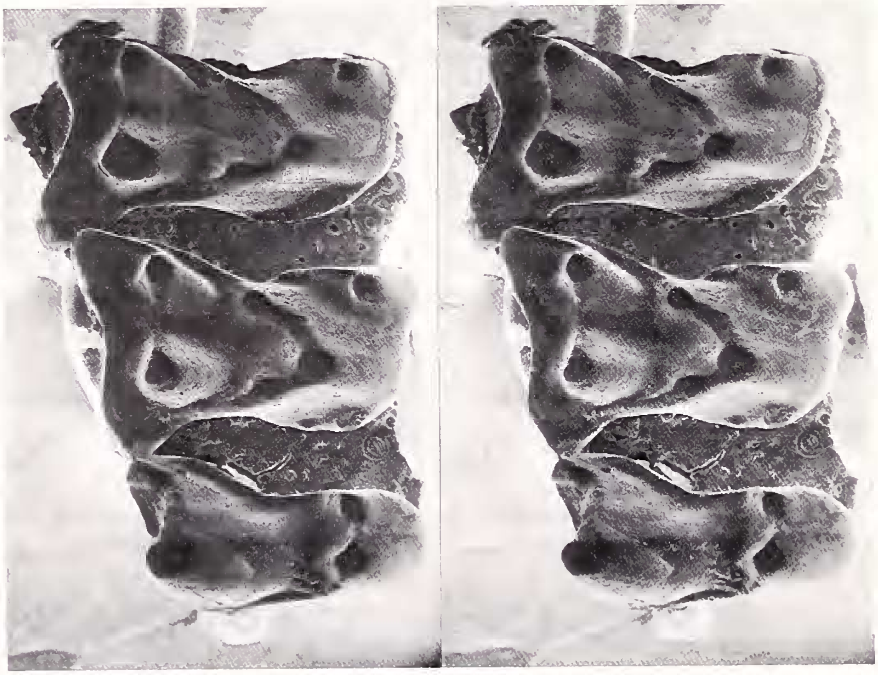
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not emarginate. The paracone, much larger and higher than the extremely reduced metacone, is linked to the tip of the parastylar salient by a weak preparacrista. Small, short anterolingual and posterolingual cingula occur basal to the protocone.

A number of isolated DP^4s have tentatively been identified from the Powder Wash collection, based on morphological and size association with known parts of the dentition of *S. edenensis*. DP^4s thought to pertain here are molariform teeth, triangular in occlusal view and much longer buccally than lingually, relative to P^4, M^{1-2}. The paracone and metacone are rounded and conical, with the paraconid slightly taller and larger. The protocone and the conules are sharp, crescentic cusps with equally distinct protocristae and conulecristae. As on M^1, the ectoflexus is shallow, and the posterior cingulum is developed as a broad shelf that terminates in a hypocone lingual and basal to the protocone. However, the hypocone is much smaller relative to M^{1-2}, and the lingual contour of the crown is continuous. On M^{1-2} of *S. edenensis*, a valley occurs lingually between the bases of the protocone and hypocone. A small parastyle occurs on the parastylar salient of DP^4, which juts anteriorly beyond the remaining anterior margin of the crown. As on P^4, M^{1-2}, the post-metacrista is developed as a high crest running from the metacone to the tip of the expanded metastylar salient. A preparaconulecrista extends to the parastyle and defines a narrow paracingulum along the base of the paracone. Similarly, the postmetaconulecrista delineates a strong metacingulum along the posterior part of the base of the high postmetacrista.

REMARKS: The distinctions between *S. edenensis*, *S. priscus*, and another species, *S. curtidens*, are discussed in the next two sections. The large sample of *S. edenensis* from Powder Wash (early Bridgerian) exhibits a range of variation that excludes AMNH 56035, holotype of "*S. mcgrewi*" (late Bridgerian), and raises the question of the validity of the synonymy of *S. mcgrewi* and *S. edenensis* (see Table 3). Along with AMNH 56035, left maxilla with P^3-M^2, McKenna and Simpson (1959) tentatively referred AMNH 56034, partial left lower jaw with M_3, to *S. mcgrewi*. Both specimens were recovered from the same excavation in the Bridger Formation, near Tabernacle Butte. The authors contended that the lower jaw with M_3 was suitable in size and structure for occlusion with the maxilla. In the same paper, Simpson noted that the holotype of *Diacodon edenensis* (McGrew, 1959), a lower jaw with M_{1-3}, resembled *Scenopagus* more than the leptictid *Diacodon*, although its occlusal fit with the holotype maxilla of *S. mcgrewi* was poorer than that of the referred jaw of *S. mcgrewi*. Robinson (*in* McKenna, et al., 1962) concurred with Simpson concerning the affinities of *Diacodon edenensis* and referred that species to *Scenopagus*. However, Robinson discounted as individual variation Simpson's observed differences between the lower jaw of *S. mcgrewi* and *D. edenensis*, and synonymized all the material as *Scenopagus edenensis*. The large sample of *S. edenensis* from Powder Wash makes it difficult to attribute to individual variation alone the rather large difference in size between the type maxilla of *S. mcgrewi* and the upper limit of the size range of the upper dentition of *S. edenensis*, although the tentatively referred lower jaw of *S. mcgrewi* (AMNH 56034) falls within the upper limit of the range in size of M_3 of *S. edenensis*. Two alternative answers are suggested: The tentatively referred lower jaw of *S. mcgrewi* is actually *S. edenensis*, and AMNH 56035 remains the type and only known specimen of *S. mcgrewi*; or the large range in variation of the lower dentition of *S. edenensis* is artificial and actually represents two distinct populations. There is some basis for the latter suggestion. The type material of *S. mcgrewi* and *S. edenensis* was recovered from deposits in the upper part of the Bridger Formation. The referred sample of *S. edenensis* came from the early Bridgerian Green River Formation. Examination of the measurements of lower dentitions referred by Robinson (1966) and West (1973) to *S. edenensis* shows that specimens recovered from the Upper Bridger deposits fall within the upper part of the size range, whereas those from the Lower Bridger horizons, as well as those from the temporally equivalent Powder Wash locality, make up the lower part of the size range. Thus, the Upper Bridger material may represent typical *S. edenensis*, whereas that from lower Bridgerian and equivalent localities may represent a smaller population of *S. edenensis*, or a smaller species of *Scenopagus*. Unfortunately, almost all remains of upper dentition referrable to *Scenopagus* have been recovered from early Bridgerian horizons in Wyoming and Utah. Apart from the type maxilla of *S. mcgrewi*, only West (1973) has reported upper teeth of *Scenopagus* from Upper Bridger localities,

◀Fig. 4. *Scenopagus edenensis*, Green River Formation, Utah. (A) CM 17318, RP_3-M_1, approx. X 12; (B) CM 6449, RM_{1-3}, approx. X 12; (C) CM 6433, LP^4-M^2, approx. X 14.

and these correspond well to the size range of upper teeth from Powder Wash that are here identified as *S. edenensis.* Except for size, all material from early and late Bridgerian horizons referred here and elsewhere to *Scenopagus edenensis* and *S. mcgrewi* is structurally identical. Consequently, all the material is referred to *S. edenensis,* although we may be dealing with a series of temporal subspecies from the Late Wasatchian through the Late Bridgerian.

Scenopagus priscus (Marsh, 1872)

(Fig. 5; Tables 2, 3)

TYPE: YPM 13509, Bridger Formation, Wyoming.

REFERRED SPECIMENS: P^4: TTU-P- 7051; M^1: TTU-P- 7060, 7078, 7075, 7074, 7077, 7062, 7073, 7080, 7076, 7059, 7057, 7053, 7066, 7068, 7065, 7055, 7069, 7071, 7056, 7072, 7079, 7064, 7067, 7070, 7063, 7061, 7058; CM 30784; M^2: TTU-P-7101, 7102, 7116, 7112, 7106, 7109, 7107, 7115, 7108, 7113, 7110, 7114, 7103, 7104, 7111, 7105, CM 30783; M_1: TTU-P- 7094, 7098, 7099, 7097, 7096, 7100, 9082, 7092, 7093, 7081, 7083, 7085, 7090, 7095, 7087, 7086, 7088, 7120, 7121, 7119; M_2: TTU-P- 7124, 7125, 7117, 7118, 7089, 7122, 7129, 7131, 7132, 7130, 7126, 7127; M_3: TTU-P- 7128, 7123, 7137, 7140, 7138, 7139, 7135, 7142, 7134, 7141, 7143, 7136. CM 13753, LP_4-M_1; CM 13749, LM_{1-2}; CM 13750, RP_4-M_1; CM 13744, P_4; CM 17316, M_{2-3}; CM 13746, LM_1; CM 13743, LM_{2-3}; CM 13748, M_{1-2}; CM 6486 RP_4-M_2; CM 17319, LM_{2-3}; CM 13751, LP_4-M_2; CM 13752, LP_4-M_1; AMNH 56060, LM_{1-3}; AMNH 55156, LP_4-M_1.

LOCALITIES: Locality III, Huerfano Formation, Colorado; Powder Wash, Green River Formation, Utah; Henry's Fork and Hyopsodus Hill, Bridger Formation (Upper), Wyoming.

KNOWN DISTRIBUTION: Late Bridgerian, Wyoming; early Bridgerian, Utah; late Wasatchian, Colorado.

DESCRIPTION AND REMARKS: *S. priscus* closely resembles *S. edenensis* in known parts of the dentition, but is much smaller and bears a number of diagnostic differences in cusp morphology. On P_4 of *S. priscus,* the paraconid is flange-like and the talonid is usually narrower than the trigonid. M_3 of *S. priscus* is much reduced relative to M_2, the ectoflexus on M^2 is deep, and the lingual groove between the bases of the hypocone and protocone on M^{1-2} is weak. In contrast, the paraconid on P_4 is more nearly cuspate and distinct in *S. edenensis,* and the talonid is generally wider than the trigonid. M_3 of *S. edenensis* is unreduced, but elongate relative to M_2. The labial emargination of M^2 is relatively shallow, and the lingual indentation between the bases of the hypocone and protocone on M^{1-2} is pronounced.

McGrew and Sullivan (1970) first described putative upper teeth of *S. priscus.* Although these teeth from Bridger A are very similar to upper molars of *S. priscus* from Powder Wash, they are significantly larger and are here referred to *S. curtidens,* a species of *Scenopagus* described below. Apart from size, the M^1s and M^2s discussed by McGrew and Sullivan differ from *S. priscus* in possessing a more pronounced indentation between the bases of the hypocone and protocone, and a shallower emargination of the labial border of the crown.

AMNH 11488, previously referred to *S. priscus* (Robinson, 1966), is here and elsewhere (Russell, et al., 1975) identified as *Talpavus nitidus.* The latter authors also referred AMNH 55156 from Huerfano to *Talpavus* sp. In contrast to *Talpavus,* P_4 on AMNH 55156 bears a basined talonid. I follow Robinson (1966) in retaining that specimen in *S. priscus.* The distinctions between *Scenopagus* (especially *S. priscus*) and *Talpavus* are described below in the section dealing with the latter genus.

The type of *S. priscus,* listed by Robinson (1966: Table 4) as YPM 15309, should read YPM 13509.

Scenopagus curtidens

(Matthew, 1909), new combination

(Fig. 6; Tables 2, 3)

Nyctitherium curtidens Matthew, 1909

TYPE: AMNH 12055, partial left mandible with M_{1-3}, from Henry's Fork locality, Bridger Formation (Upper), Wyoming.

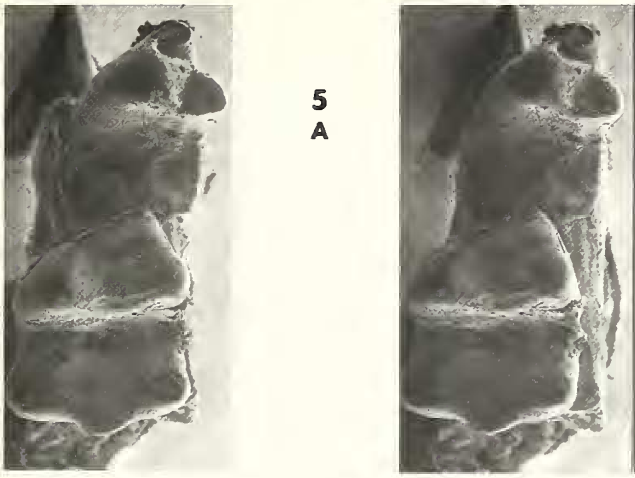
REFERRED SPECIMENS: YPM 15254, RP_4-M_3; YPM 16913, LM_{1-2}; YPM 14939, LM_{1-2}; YPM 13610-a, RP_4; YPM 13610-b, LP_4-M_2; YPM 13610-2, LM_{1-2}; YPM 15255, LM_{2-3}; YPM 16912, LP_4-M_1; YPM 16914, RM^2; AMNH 12058, RM_{2-3}; AMNH 12062, LM_{1-3}; AMNH 12064, RP_4-M_1; AMNH 11491, RM_1; AMNH 59643, RM_1; AMNH 48183, RP_4, M_2; TTU-P-3928, RM_{1-3}; TTU-P- 7054, RM_1; UCMP 96155, LM_{1-3}.

LOCALITIES: Henry's Fork, Twin Buttes, Lone Tree, and Dry Creek, Bridger Formation (Upper), Wyoming; North Leavitt Ranch, Bridger Formation (Lower), Wyoming; unknown localities, Bridger Formation, Wyoming; Cattail Spring, and Point Gulch, Bridger Formation (Upper or Lower), Wyoming; Quarry 88, Almagre facies, San Jose Formation, New Mexico; Alheit Quarry, Hiawatha Member, Wasatch Formation, Colorado; Friars Formation, California.

KNOWN DISTRIBUTION: Bridgerian, Wyoming; Wasatchian, New Mexico; early Wasatchian, Colorado; early Uintan, California.

DESCRIPTION: The type and referred specimens exhibit features characteristic of *Scenopagus,* but morphologically intermediate between *S. edenensis* and

Fig. 5. *Scenopagus priscus,* Green River Formation, Utah (A) CM 13752, LP_4-M_1, approx. X 20; (B) CM 13749, LM_{1-2}, approx. X 15; (C) CM 17319, LM_{2-3}, approx. X 14; (D) CM 30784, RM^1, approx. X 12 (E) CM 30783, LM^2, approx. X 12. Fig. 6. *Scenopagus curtidens,* Bridger Formation, Wyoming. (A) YPM 15254, RP_4-M_3, approx. X 12; (B) YPM 16914, RM^2, approx. X 10. ▶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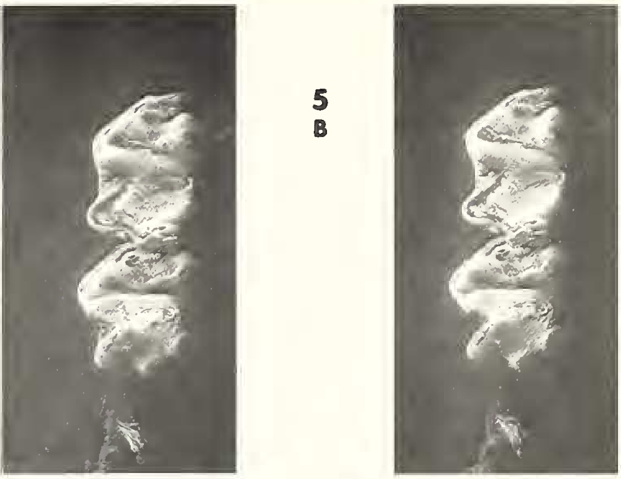
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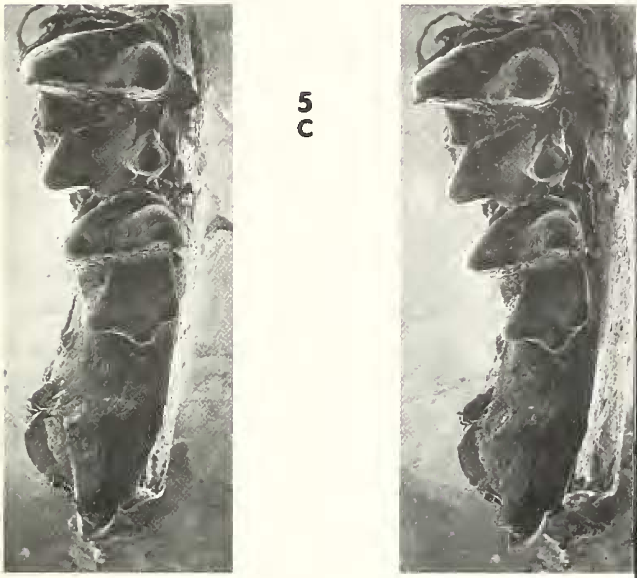
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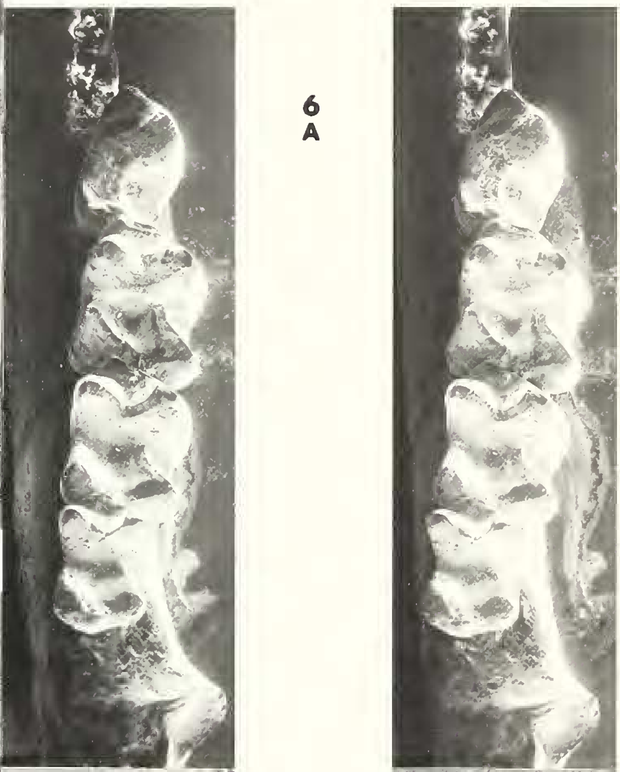
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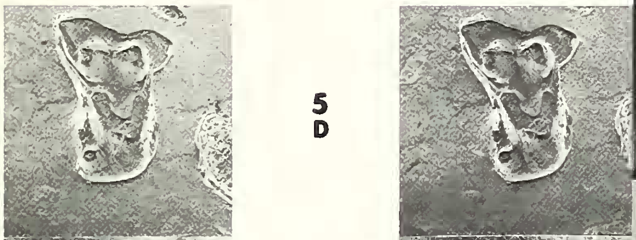
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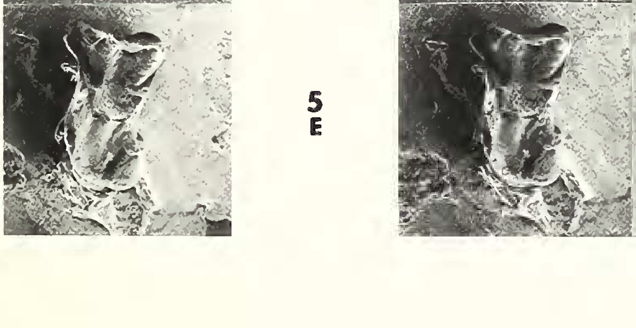
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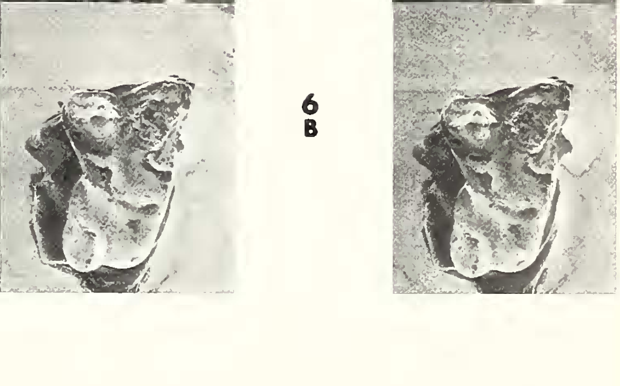
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Table 2. Dimensions of lower teeth of *Scenopagus edenensis, S. curtidens* and *S. priscus*

	P_4		M_1			M_2			M_3		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
S. edenensis	2.0- 2.4	1.4- 1.6	2.1- 2.4	1.7- 1.9	1.7- 2.0	2.1- 2.7	1.8- 2.2	1.8- 2.0	2.2- 2.7	1.7- 1.8	1.2- 1.5
Mean	2.06	1.48	2.23	1.80	1.83	2.25	1.96	1.84	2.38	1.72	1.34
N.	10	9	13	13	12	22	19	19	19	9	9
SD.	0.8		0.12	0.09	0.16	0.22	0.14	0.11	0.35		
CV.	3.93		5.78	5.07	9.01	9.79	7.41	5.97	14.79		
S. curtidens	1.5- 1.6	1.1- 1.2	1.7- 2.0	1.4- 1.6	1.5- 1.6	1.7- 1.9	1.5- 1.7	1.4- 1.6	1.5- 1.7	1.2- 1.3	0.9- 1.2
Mean	1.52	1.18	1.82	1.49	1.53	1.77	1.58	1.46	1.60	1.26	1.04
N.	6	6	11	11	14	12	11	12	5	7	5
SD.			0.07	0.08	0.07	0.06	0.10	0.12			
CV.			3.88	6.00	4.78	3.79	6.32	8.24			
S. priscus	1.2- 1.4	0.9- 1.1	1.3- 1.5	0.8- 1.3	0.9- 1.3	1.4- 1.6	1.1- 1.3	0.8- 1.2	1.3- 1.5	0.8- 1.1	0.6- 0.8
Mean	1.30	0.96	1.43	1.04	1.11	1.45	1.20	1.04	1.33	0.95	0.72
N.	6	7	31	31	29	18	18	17	15	15	12
SD.			0.07	0.07	0.06	0.06	0.07	0.03	0.04	0.07	0.05
CV.			5.40	7.23	5.87	4.09	6.39	3.39	3.48	7.92	7.25

S. priscus. As in *Scenopagus*, the paraconid and metaconid on the premolariform P_4 are lower than (and merged with) the protoconid, and the talonid is essentially unicuspid, short and basined. On M_{1}-$_{3}$ the paraconid is compressed into a low, broad paracristid, and the metaconid and protoconid are large, rounded cusps, with the metaconid slightly taller. The cristid obliqua originates labially on the posterior wall of the trigonid. The hypoconid, lower than the high, conical entoconid, becomes flat with wear and the hypoconulid occurs lingual to the midline. The talonid extends farther labially than the trigonid on M_1, but is narrower than the trigonid on M_{2}-$_{3}$. Two mental foramina occur on the mandible, one below P_4 and P_3, respectively.

S. curtidens is intermediate in size between *S. priscus* and *S. edenensis*, but is closer to *S. priscus* in the smaller, less cusp-like nature of the paraconid on P_4, a talonid narrower than the trigonid on P_4, and a reduced M_3 relative to M_2. Also, the single M^2 referred here to *S. curtidens*, and the upper molars described by McGrew and Sullivan (1970) as *S. priscus*, are virtually identical to upper molars of *S. priscus*, except that they are larger and possess a deeper valley between the lingual faces of the hypocone and protocone, and a shallower labial emargination.

YPM 13610-a, 13610-b, and 14939, previously referred to *S. priscus* (Robinson, 1966) are here placed in *S. curtidens*.

REMARKS: *S. edenensis*, *S. curtidens*, and *S. priscus* were contemporaneous during the Bridgerian and Late Wasatchian. Only *S. curtidens* has been recognized from earlier deposits. The reduction of the M_3 in *S. curtidens* and *S. priscus* may be a derived feature, relative to the retention of an unreduced M_3 in *S. edenensis*. With premolarization of P_4, the species of *Scenopagus* could have radiated from a Paleocene adapisoricid like *McKennatherium ladae*.

Ankylodon

The genus *Ankylodon* is known from the Late Eocene (Setoguchi, MS thesis) and Oligocene [(Galbreath,

Table 3. Dimensions of upper teeth of *"Scenopagus mcgrewi," S. edenensis, S. curtidens* and *S. priscus*

	P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W
"S. mcgrewi"	2.8	3.3	2.8	3.7 est.	2.5 est.	3.9		
S. edenesnsis	2.0	2.6-2.9	2.1-2.4	3.0-3.3	2.0-2.2	3.1-3.5	1.5-1.9	2.6-2.8
Mean	2.0	2.69	2.25	3.18	2.10	3.31	1.67	2.73
N.	6	7	8	11	6	7	3	3
SD.				0.09				
CV.				2.66				
S. curtidens					1.5	2.5		
S. priscus	1.4	2.0	1.4-1.6	1.9 2.2	1.1-1.4	1.9-2.2		
Mean			1.47	2.06	1.32	2.09		
N.	1	1	15	17	6	7		
SD.			0.07	0.07				
CV.			4.81	3.64				

1953; Lillegraven and McKenna, (MS); Patterson and McGrew, 1937)] of North America. Excellent material comprising most of the upper and lower dentition of a Chadronian species of *Ankylodon* is presently being described by Lillegraven and McKenna (MS). The authors have kindly allowed me access to the manuscript and casts of the material. The dental morphology of *Ankylodon* mirrors that of *Scenopagus* as follows: P_1 and P_2 are single-rooted and unicuspid. P_3 and P_4 are double-rooted, possess a large protoconid, a small paraconid, and a short, shallow-basined talonid with a tiny hypoconid. A metaconid is lacking on P_3 and is present, but lower than the protoconid on P_4. The talonid is wider than the trigonid on M_1 but narrower on M_{2-3}. On M_{1-3} the paraconid is anteroposteriorly compressed into a strong low paracristid, the metaconid is taller and larger than the protoconid, the cristid obliqua is labial on the posterior wall of the trigonid, the hypoconid is lower than the high conical entoconid, and becomes flat with wear, and the hypoconulid occurs slightly lingual to the midline. On M_3 the talonid is elongate, and the hypoconulid projects posterodorsally.

As in *Scenopagus*, P^4 of *Ankylodon* lacks conules and bears a tall, central paracone, a lower lingual protocone, a small hypocone on the postprotocrista, a small anterior parastylar salient, a large metastylar expansion, and a high postmetacrista. The crown is essentially T-shaped with an anteroposteriorly expanded lingual end. M^{1-2} are very transverse, with a large valley separating the bases of the hypocone and protocone lingually. The postcingulum is strong and shelf-like and bears a large hypocone. The postmetacrista is high, the buccal margin of the crown is deeply emarginate medially, and the stylar salients are expanded. M^3 lacks a hypocone, is smaller than M^2, and possesses a large paracone and an extremely reduced metacone.

As Russell, et al. (1975) also noted, the features that distinguish *Ankylodon* from *Scenopagus* are not unique, but represent the elaboration of certain characters in *Ankylodon* beyond the condition seen in *Scenopagus*. Compared to *Scenopagus*, P_1 of *Ankylodon* is relatively higher, but P_2 is reduced. P_3 possesses a taller protoconid, a more distinct paraconid, and a longer, wider, better-developed talonid. Similarly, on P_4, the protoconid and metaconid are higher and more conical. The paraconid, although not cuspate, is much larger and projects more anteriorly from the base of the trigonid, and the talonid is more elongate. On M_{1-2} of *Ankylodon,* the trigonids are more anteroposteriorly compressed, the protoconid and metaconid are taller, sharper cusps; the talonid is longer, the hypoflexid is deeper, and the cristid obliqua is more arcuate. On known parts of the upper dentition, *Ankylodon* differs from *Scenopagus* as follows: P^3, much more transverse (buccolingually) and elongate (anteroposteriorly), with longer parastylar and metastylar salients, resembles a "T" instead of a triangle in occlusal outline, and is more nearly semimolariform. The paracone on P^3 is much larger and taller, the protocone is more prominent, and a small metacone is present. On P^4, the lingual half of the crown is longer (anteroposteriorly), the protocone and paracone are taller, more spire-like, and the postmetacrista is higher and bears a tiny metacone. On M^{1-2} the hypocone and postcingulum are considerably enlarged, the lingual furrow between the hypocone and protocone is deeper and wider, the conules are larger, and the buccal edge of the crown is more emarginate. The metastylar salient is more expanded on M^1, the parastylar area is greater on M^2, and on M^3 the parastylar salient is greatly reduced relative to *Scenopagus.*

In effect, features that are diagnostic of *Scenopagus* are equally descriptive of *Ankylodon,* except for larger and higher, more nearly conical cusps, sharper, broader cingula, larger metastylar and parastylar salients on M^1 and M^2, respectively, and greater anteroposterior compression of the trigonid on M_{1-3}. These differences between Bridgerian *Scenopagus* and Uintan-Chadronian *Ankylodon* may be a consequence of a continuation of similar trends in the same dental characters seen in the evolution of Wasatchian-Bridgerian species of *Scenopagus* from the Paleocene *McKennatherium.* Butler (1972) suggested, and I concur, that *Ankylodon* is the latest known adapisoricid. Comparison of *Ankylodon* with *Scenopagus* indicates that the ancestry of *Ankylodon* lies among the Bridgerian species of *Scenopagus*—a conclusion that Robinson and McKenna have also come to independently (McKenna, personal commun. 1975).

The lower dentition of *Ankylodon,* completely preserved on the AMNH "dark" specimen (Lillegraven and McKenna, MS), consists of three molars and seven antemolar teeth. As traditionally interpreted, the lower dental formula is $I_{2-3}C_1P_{1-4}M_{1-3}$. However, the homologies of the anterior teeth are uncertain, and alternate interpretations of the lower antemolar dental formula are possible. Since the tips of both I_2 and I_3 are broken off, the identification of these teeth as incisors is tentative. I_2 is round and I_3 is oval in cross section. Both teeth are enlarged and project anterodorsally. I_3, larger than I_2, is concave along the posteromedial and posterolabial face of the crown, and bears a posterobasal cuspule. Relative to I_2, the morphology of I_3 may be interpreted as caniniform. The third tooth in the jaw—the alleged C_1—is structurally identical to, and as premolariform as, the alleged P_1, and as such, is the first of five premolariform teeth. These identifications can yield a lower antemolar dental formula of either $I_3C_1P_{1-5}$, or, if the two anterior lower teeth are incisors, $I_{2-3}P_{1-5}$. Some of the premolars may be retained deciduous teeth, as has been postulated for other preptotheres (McKenna, 1975). A fourth possible interpretation of homologies, which also pertains to the discussion below of the erinaceid *Litolestes ignotus,* concerns the identification of the third tooth in the jaw—the premolariform "canine." McDowell (1958: 157, Fig. 19A), has identified the deciduous C_1 in the insectivore *Nesophontes* as a premolariform, single-rooted tooth, which is very similar to the premolariform "canine" of *Ankylodon* (and *Litolestes ignotus*). However, calling this tooth dC_1 in *Ankylodon* (in an antemolar dental formula of $I_{2-3}dC_1P_{1-4}$) is premature, since the homology of this tooth locus in *Nesophontes* is perhaps also uncertain. The alleged permanent canine of *Nesophontes* is not caniniform, but, like its milk predecessor, is premolariform (McDowell, 1958: 157, Fig. 19C), and may represent a permanent premolar with a deciduous premolariform predecessor. The lower antemolar dental formual of *Ankylodon* is tentatively identified as: I_2, I_3 or C_1, $dP_1P_2P_3P_4P_5$. Clearly, until more complete material of the anterior dentition of *Ankylodon* and other adapisoricids is recovered, the homologies of the anterior teeth remain unsettled.

Macrocranion Weitzel, 1949

The genus *Entomolestes* was described by Matthew (1909) from the Middle Eocene Bridger Formation, with *E. grangeri* as the type species. Subsequently, Matthew (1918) named a second species, *Entomolestes nitens,* from the Early Eocene Willwood Formation. Since then, definite and tentative occurrences of *E. nitens* have been recorded from the Wasatch Formation, Colorado (McKenna, 1960a), the early Wasatchian Powder River local fauna, Wyoming (Delson, 1971), the Lysite and Lost Cabin Members, Wind

River Formation, Wyoming (Guthrie, 1967, 1971), the Wasatchian Almagre facies of the San Jose Formation, New Mexico (Robinson, 1968b), and Sparnacian-Cuisian localities in France (Russell, et al., 1975). No additional material referrable to *E. grangeri* has been recovered since its original description.

Robinson (1968b) and Butler (1972) suggested that *E. nitens* was generically distinct from *E. grangeri* and should be referred to *Scenopagus*. Guthrie (1971) disagreed, citing differences between *E. nitens* and *Scenopagus* in the structure of the upper molars, and retained the use of *E. nitens*.

From examination of the type, paratype, and a large amount of material referred to *E. nitens*, it is clear that Robinson (1968b) and Butler (1972) were correct in observing the generic disparity between *E. grangeri* and *E. nitens*. Perhaps the affinities of the former, as discussed in a later section, are with the Erinaceidae. Although P_4 in both species is similarly premolariform, the talonid is much shorter on that of *E. grangeri*. $M_{1\text{-}3}$ of *E. grangeri* have less robust cusps, comparatively shorter talonids with more nearly straight posterior margins, more triangular trigonids, reduced hypoconulids, and shallower talonid basins, compared to *E. nitens*.

As described below, *E. nitens* is also distinct from *Scenopagus*, but is virtually identical to *Macrocranion tenerum* (= *Messelina*) hitherto known only from the middle Eocene of Europe. *Macrocranion* was shown by Tobien (1962) to be a senior synonym of *Aculeodens* and was referred to the Amphilemuridae of McKenna (1960a), although Van Valen (1967) considered the genus to be a creotarsine adapisoricid. *Messelina tenera* (Tobien, 1962) was recently, and I think correctly, referred to *Macrocranion* (as *M. tenerum*) by Russell, et al. (1975). These authors have also commented on the remarkable similarity between *E. nitens* and *Macrocranion*, especially in the lower dentition. Except for the occurrence of a posterior cingulid on $M_{1\text{-}2}$ of *M. tenerum*, distinction between that species and *E. nitens* is difficult. Nonetheless, Russell, et al. (1975), claimed that the presence of a tiny metacone on P^4 of *E. nitens* from Four Mile, as well as the greater transverse nature of $M^{1\text{-}3}$ compared to *Macrocranion* warranted generic separation of the two species. But, as described below, P^4 of *E. nitens* from the Almagre does not possess a metacone. Although I have not examined the original material of upper molars of *Entomolestes* cf. *nitens* from Europe (Russell, et al., 1975), the illustrations imply that part of the hypodigm (notably, Mu-118-L, Av-841-Bn) may be referrable to *Scenopagus*, upper molars of which are indeed more transverse than those of *E. nitens*. M^1 of *M. tenerum* as figured in Tobien (1962) is similar in crown proportion to that of *E. nitens*. The reconstruction and figures of $M_{2\text{-}3}$ of *M. tenerum* are apparently inaccurate (Russell, et al., 1975). *E. nitens* and *E.* cf. *nitens* from the early Eocene of North America and Europe are here considered species of *Macrocranion*.

Macrocranion nitens

(Matthew, 1918), new combination

(Fig. 7; Tables 4, 5)

TYPE: AMNH 15697, partial right mandible with P_4-M_2 from the Willwood Formation, Big Horn Basin, Wyoming.

PARATYPE: AMNH 14674, partial right mandible with ½ P_4-M_3 from the Lysite Member, Wind River Formation, Wyoming.

REFERRED SPECIMENS: AMNH 48187, RM_3; AMNH 48174, RP_4-M_3; AMNH 48188, frag. P_4; AMNH 48179, RP_4-M_2; AMNH 48189, LP_4-M_2; AMNH 48181, frag. talonid; AMNH 48176, LP_4-M_3; AMNH 48182, RM_2; AMNH 48172, $LM_{2\text{-}3}$; AMNH 48178, LP_4-M_3; AMNH 48180, RP_4-M_2; AMNH 48184, $RM_{1\text{-}2}$; AMNH 48177, LP^4-M^2; AMNH 48175, $RM^{1\text{-}2}$; TTU-P- 4211, RP_4-M_2; CM 12398, $LM^{1\text{-}3}$; CM 22019, RM^2; CM 22014, $LM_{2\text{-}3}$.

LOCALITIES: Quarry 88, Almagre facies, San Jose Formation, New Mexico; Lysite and Lost Cabin Members, Wind River Formation, Wyoming; Willwood Formation, Big Horn Basin near Otto, Wyoming.

KNOWN DISTRIBUTION: Wasatchian, New Mexico, Wyoming.

DESCRIPTION: The description presented here is based on the holotype, the paratype, and the single quarry sample from the Almagre. Teeth anterior to P_3 and P^4 are unknown. P_3 is a single-rooted, very small, peg-like tooth, with one laterally compressed, anterior-leaning cusp.

P_4 is variable in structure, more so than the lower molars, and more than has been noted in previous descriptions. It is a large, two-rooted premolariform tooth with a three-cusped trigonid and lower, shorter, talonid. The protoconid is large and robust, leans posteriorly, and occupies most of the basal area of the trigonid. The paraconid is low, conical, and arises from the anterolingual part of the base of the protoconid. The two cusps are continuous labially, but are demarcated lingually by a weak vertical groove. A paracristid extends down the anterior face of the protoconid to the paraconid, joining the two cusps along the entire height of the paraconid. The metaconid, slightly higher than the paraconid, but only one-third the height of the protoconid, occurs low on the posterolingual face of the protoconid, and varies in size from a small bulge (on the holotype AMNH 15697) to a conical cusp (on the Almagre specimens). In the latter condition a V-shaped notch separates the metaconid and protoconid.

The structure of the talonid of P_4 is most variable. On all specimens examined, the talonid is low, as wide as, or wider than, the trigonid basally, and approximately one-half as long. An extremely weak cristid obliqua extends directly posteriorly from the trigonid to a raised point (?hypoconid) on the posterior rim of the talonid, and delimits the labial margin of a shallow talonid basin. The width of the basin from the lingual margin of the talonid to the cristid obliqua represents only the lingual one-third of the total basal width of the talonid. A hypoflexid groove for occlusion of the paracone of P^4 slopes very gently labioventrally from the cristid obliqua to the basal margin of the talonid. Since the cristid obliqua is very weak, it is almost obscured by wear on many of the specimens. On some of the material from the Almagre, an additional cuspule occurs on the raised posterior rim of the talonid basin in the position of an entoconid. A precingulum, when present, is weak and short. These variations seem taxonomically insignificant, and in each case, the P_4 is associated in a partial mandible with molars of *M. nitens.*

The molars of *M. nitens* are large, robust teeth that lean lingually, and are almost rectangular in occlusal outline. The talonid is longer and only slightly lower than the trigonid on M_{1}-$_{3}$, and wider than the trigonid on M_{1}-$_{2}$. A slight lateral constriction occurs basally between the trigonid and talonid. The protoconid and metaconid are low, conical, almost bulbous cusps, with the metaconid slightly larger and taller. A strong, broad paracristid runs anterolingually from the anterior face of the protoconid, and terminates well anterior to the metaconid, so that the trigonid is open lingually. The paraconid is a barely discernible bulge, anteroposteriorly compressed at the lingual end of the paracristid.

The talonid on M_{1}-$_{3}$ bears a large, rounded entoconid, almost as tall as the metaconid, and a much lower hypoconid that becomes flat with wear. On M_{1}-$_{2}$, the hypoconulid is low, small, and occurs slightly lingual to the midline on the same wall as the entoconid. On M_3 the hypoconulid is medial, distinct, as large as the entoconid, and projects posterodorsally. The cristid obliqua is long, broad, and strong, and originates directly below the notch between the protoconid and metaconid. The hypoflexid notch is shallow, the precingulid is very weak, and a postcingulid does not occur. Characteristically, on M_1 the labial part of the base of the trigonid bulges anterolabially and the paracristid is sharply angled at the anterior part of the base of the protoconid. This lends the M_1 trigonid a very squared appearance in occlusal view, relative to the more nearly triangular trigonid on M_{2}-$_{3}$. Similarly, the base of the talonid below the hypoconid on M_{1}-$_{2}$ is expanded labially and posteriorly.

Upper dentitions of *M. nitens*, although noted from Lost Cabin (Guthrie, 1971) and from the Almagre (Robinson, 1968b), have never been adequately described. Two specimens, AMNH 48177 and AMNH 48175, comprising P^4-M^3 and $M^{1\text{-}2}$ respectively, occur in the single quarry sample of *M. nitens* from the Almagre.

Only the labial half of P^4 is preserved on AMNH 48177. The broken crown bears a very large, tall, and conical paracone, a small anterolabial parastyle, and a short posterolabial metastylar salient. The paracone is approximately twice as high and large as that on $M^{1\text{-}2}$. There is no evidence of a metacone on P^4, although a weak crest runs vertically along the posterior face of the paracone to the tip of the metastylar salient. The buccal margin of the crown is shallowly convex labially.

$M^{1\text{-}2}$, essentially rectangular in occlusal outline, are not transverse and are only weakly constricted anteroposteriorly across the conules. The buccal borders of the crowns are shallowly emarginate and the lingual margins are oriented posterolingually. The parastylar and metastylar areas are small and not expanded, although the parastylar salient on M^1 juts anteriorly beyond the remaining anterior margin of the crown. The paracone and metacone, low, subequal, conical cusps, are well separated and occur close to the labial border of the crown, leaving virtually no stylar area. The protocone is low, pyramidal, only slightly compressed anteroposteriorly, and forms the anterolingual corner of the crown. The hypocone, rounded and conical, is only slightly lower than, but almost as large as, the protocone, and forms the posterolingual corner of the crown. A shallow lingual valley between the protocone and hypocone divides the lingual length of the crown into approximately equal halves. A weak crista extends anterolabially from the hypocone to the anterior wall of the trigon below the preprotocrista. The conules are low, but well developed, conical and subequal, and are linked to the protocone by strong protocristae. The preparaconulecrista and postmetaconulecrista are weakly developed, but extend to the parastyle and metastyle, respectively, and delineate a narrow paracingulum and metacingulum. The postmetacrista is weak, low, and not crest-like. A short narrow precingulum occurs on $M^{1\text{-}2}$.

M^3, triangular in occlusal aspect, has a greatly reduced metastylar area and a relatively tiny metacone, approximately two-thirds the size of that of M^2. The paracone and parastylar salient are unreduced relative to M^2. M^3 lacks a hypocone, and the postcingulum is very short.

REMARKS: *Macrocranion nitens* and *Scenopagus* are easily distinguished in known parts of the dentition, although P_4 and the upper molars are similar in both forms. In contrast to *Scenopagus*, the metaconid on P_4 of *M. nitens* is more nearly separate from the protoconid, the cristid obliqua is considerably weaker, the posterolabial part of the base of the talonid is expanded, the posterior rim of the talonid basin is raised, and the slope of the hypoflexid groove is lower.

Compared to *Scenopagus*, M_{1-3} of *M. nitens* are lower, their bases are fattened labially (exodaenodonty), the trigonid is much lower relative to the talonid, the talonid is proportionately wider and considerably longer than the trigonid, and the cusps are lower and more bulbous. In *M. nitens*, the paraconid is better developed, more anterior and not as close to the metaconid, the trigonid on M_1 is open lingually and more nearly square in occlusal outline, the hypoconid is less compressed anteroposteriorly, the cristid obliqua is longer and meets the trigonid more lingually, and the precingulid is weaker.

P^4 of *M. nitens* differs from *Scenopagus* in having a convex labial margin, very small stylar salients, and a much weaker, lower paracone-metastylar crest. The upper molars of *M. nitens* are less transverse, more nearly rectangular in occlusal outline, and less constricted across the conules. The labial margins of the molars are less emarginate, the stylar areas are much smaller and not expanded, and the cusps are lower and more nearly conical. In *M. nitens*, the hypocone is higher relative to the protocone and occupies more of the lingual area of the crown, the postmetacrista is much weaker and less crest-like, and the metacingulum is narrower.

Macrocranion cf. *M. nitens*

(Fig. 8; Tables 4, 5)

REFERRED SPECIMENS: AMNH 59673, LP_4-M_3; AMNH 59662, RP_4; AMNH 59656, RM_{2-3}; AMNH 59663, RP_4; AMNH 80071, RM_1; AMNH 59679, RP_4-M_1; AMNH 59651, RP_4; AMNH 59688, LP_{3-4}; AMNH 88846, LM_1; AMNH 88834, RM_1; AMNH 88839, LM_1; AMNH 88830, LM_{1-2}; AMNH 56318, RP_{3-4}; AMNH 59678, RP^4-M^2; AMNH 88837, LM^1.

LOCALITIES: E. Alheit, Despair and Kent Quarries, Four Mile local fauna, Hiawatha Member, Wasatch Formation, Colorado; Powder River local fauna, Bozeman locality, Wyoming.

KNOWN DISTRIBUTION: Early Wasatchian, Colorado and Wyoming; Sparnacian and Cuisian, France.

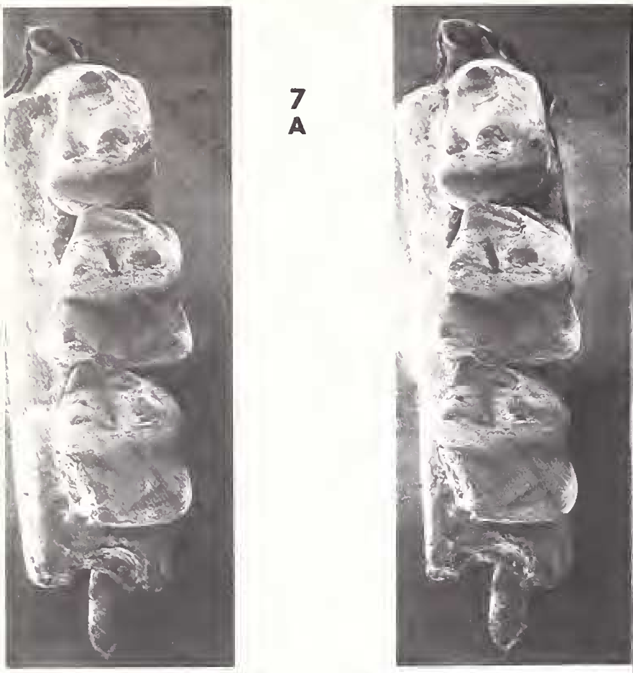
DESCRIPTION AND REMARKS: McKenna (1960a) and Delson (1971) noted the occurrence of a species of *Entomolestes* cf. *E. nitens* in the Four Mile and Powder River faunas, respectively, which was 20% smaller than the type and paratype of *E. nitens*. Although the Almagre sample of *M. nitens* increases the known variation in size of the species, the original and additional material from Four Mile is here referred to *Macrocranion* cf. *M. nitens*. This species is virtually identical to *M. nitens* in the morphology of the known parts of the dentition. The greatest difference in size occurs in the P_4, especially in the talonid. Recovery of a sizeable sample of *M. nitens* from early Wasatchian horizons should resolve the specific status of the Four Mile and Powder River material. Although the two specimens of upper dentition from Four Mile (AMNH 59678, 88837) agree in size with *M. nitens* from the Almagre, these are tentatively referred to cf. *M. nitens* on the basis of the morphology of P^4. P^4 on AMNH 59678 bears a well-developed paracone, a paracone-metastylar crest and a wear facet on this crest, where a tiny metacone occurred. This is similar to the condition on UCMP 44085 from Four Mile, which was described and figured (McKenna, 1960a) as *Entomolestes* cf. *E. nitens*. P^4 of *M. nitens* from the younger Almagre deposits lacks a metacone. Larger samples of *M. nitens* and cf. *M. nitens* may prove the presence of a tiny metacone on P^4 to be variable. If not, however, the implied loss of the metacone on P^4 during the Wasatchian in *M. nitens* would be consonant with the general trend of premolarization of P_4^4 in early Tertiary erinaceomorphs.

The isolated teeth from the Sparnacian and Cuisian of France, which Russell, et al. (1975) described as *Entomolestes* cf. *nitens*, exhibit an inordinate range of variation in size. Their structure is virtually identical to *Macrocranion nitens* and *M.* cf. *M. nitens* from North America, including the occurrence of exodaenodonty along the labial margin of M_{1-2}. It seems probable that the two species of *Macrocranion* recorded here are also represented by the material from the early Eocene of France.

Talpavus Marsh, 1872

This genus has also had a checkered history. *T. nitidus* was named by Marsh (1872) on the basis of two jaw fragments, one with $1/2M_1$-M_2, and the other with a single premolar. The latter proved to belong to *Peratherium*, a marsupial (Robinson 1968b), whereas

7
A



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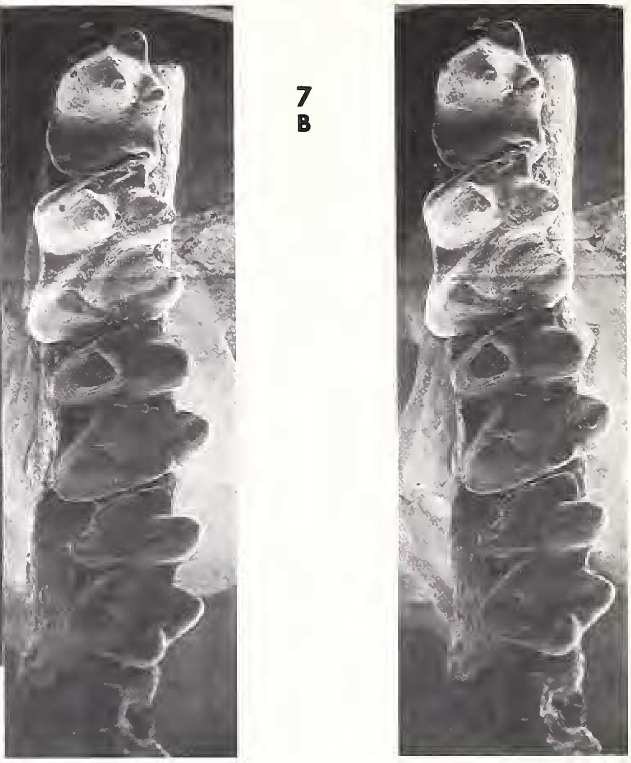

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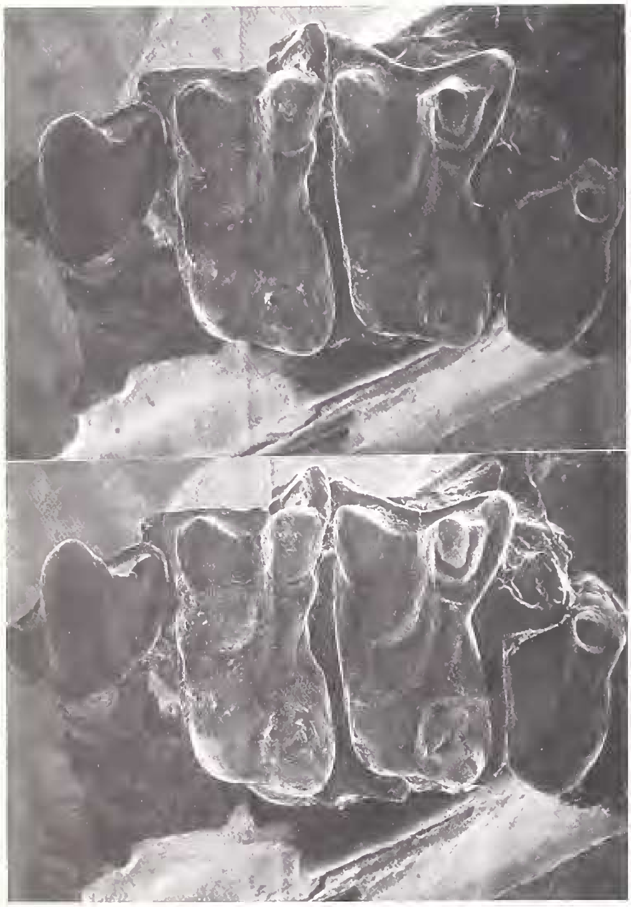

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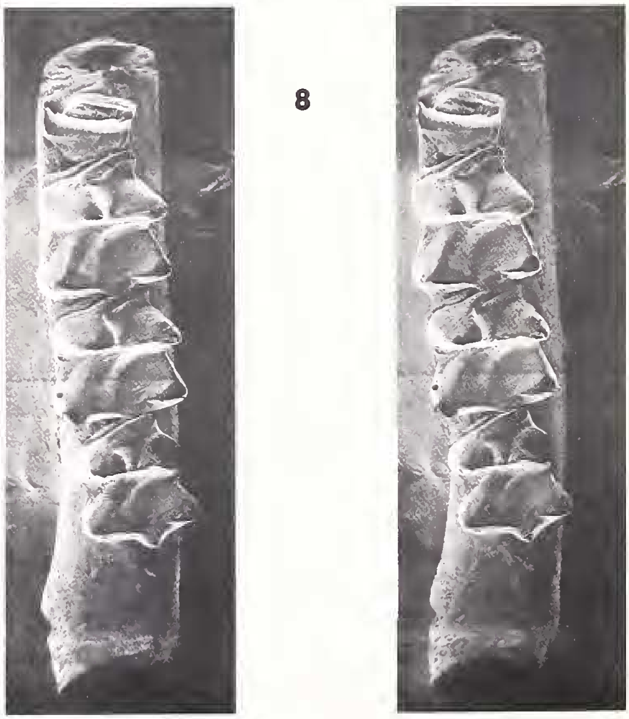


Table 4. Dimensions of lower teeth of *Macrocranion nitens* and *Macrocranion* cf. *M. nitens*

	P_4		M_1			M_2			M_3		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
M. nitens	1.6-2.0	1.1-1.3	1.9-2.1	1.3-1.5	1.5-1.6	1.8-2.1	1.4-1.6	1.5-1.7	1.9-2.2	1.2-1.4	1.3-1.4
Mean	1.77	1.20	1.94	1.43	1.54	1.96	1.49	1.60	2.06	1.30	1.35
N.	6	7	9	8	9	11	10	10	5	5	5
SD.						0.09	0.07	0.04			
CV.						4.84	5.00	2.94			
Macrocranion cf. *M. nitens*	1.4-1.7	0.9-1.1	1.6-1.8	1.3-1.4	1.4-1.5	1.7-1.8	1.4-1.5	1.5-1.6	1.7	1.2	1.3
Mean	1.47	0.97	1.76	1.36	1.47	1.73	1.43	1.53			
N.	6	6	7	7	7	3	3	3	2	1	2

Table 5. Dimensions of upper teeth of *Macrocranion nitens* and *Macrocranion* cf. *M. nitens*

	P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W
M. nitens								
AMNH 48175			—	2.5	1.8	2.5		
AMNH 48177	1.8	—	1.8	2.5	1.7	2.7	—	—
CM 12398			2.0	2.6	1.7	2.5	1.3	1.8
CM 22019					1.9	2.5		
Mean			1.90	2.53	1.78	2.55		
Macrocranion cf. *M. nitens*								
AMNH 59678	—	2.2+	1.9	2.3	1.8	2.5		
AMNH 88837			1.9	2.3				

◀ Fig. 7. *Macrocranion nitens*. (A) Type, AMNH 15697, RP$_4$-M$_2$, Willwood Formation, Wyoming, approx. X 12; (B) AMNH 48178, LP$_4$-M$_3$, San Jose Formation, New Mexico, approx. X 12; (C) AMNH 48177, LP^4-M^3, San Jose Formation, New Mexico, approx. X 16.
Fig. 8. *Macrocranion* cf. *M. nitens*, AMNH 59673, LP$_4$-M$_3$, Wasatch Formation, Colorado, approx. X 12.

the former, YPM 13511, was referred by Matthew (1909) to *Nyctitherium*. After *T. nitidus*, based on YPM 13511, was re-established as distinct from *Nyctitherium* (McKenna, et al., 1962), only four additional specimens were referred to that genus: AMNH 55686, a partial lower jaw with M_3 of *Diacodon bacchanalis* from the late Bridgerian "Hyopsodus" Hill locality; CM 12061, partial lower jaw with P_4-M_3 from Myton Pocket, Uintan of Utah (McKenna, et al., 1962): AMNH 55662, partial lower jaw with P_4-M_3 from the Huerfano local fauna, late Wasatchian of Colorado (Robinson, 1966); and YPM 16334, partial lower jaw with P_4-M_2 from the upper part of the Bridger Formation, Wyoming (Robinson, 1968b).

A second species of *Talpavus*, *T. sullivani*, was described by Guthrie (1967; 1971) from the Lysite and Lost Cabin Members of the Wind River Formation, Wyoming. A number of the teeth referred to this species are here identified as *Scenopagus*. The remaining portion of the hypodigm is distinct from *Talpavus* and needs restudy. Robinson (1968b) also referred the Paleocene *Leipsanolestes seigfriedti* Simpson, 1928, to *Talpavus* although that species had previously been allied with *Entomolestes* (McKenna, 1960a). *Leipsanolestes* is distinct from both *Talpavus* and *Entomolestes* and is discussed in a later section.

The confusion and distinction between the allegedly similar *T. nitidus* and *Entomolestes grangeri* were dealt with by Robinson (1968b). Delson (1971) recognized Robinson's criteria, but inexplicably synonymized the species of *Scenopagus* with *Talpavus*.

The major problem in defining *Talpavus* is the fragmentary nature of the type specimen, YPM 13511, and the resulting paucity of diagnostic criteria. However, four features on the type appear to me to be distinctive and indicative of its affinities: the paraconid, preserved only on M^2, is compressed anteroposteriorly into a thin, high crest that flares anterolingually at its lingual end; the entoconid is much higher than the hypoconid; the talonid and trigonid are of equal width; the hypoconulid, small and slightly lingual in position, occurs at the posterolabial part of the base of the entoconid and is delineated from that cusp by a sharp notch. The juncture of the hypoconulid and hypoconid is not as well marked, and with wear, the two cusps are joined by a hypocristid. The first two characters align the type of *T. nitidus* with adapisoricids; the latter ones distinguish it from *Scenopagus priscus*, the adapisoricid most similar in size and structure to *T. nitidus*. On M_2 of *S. priscus* the talonid is narrower than the trigonid, the hypoconulid is larger and more clearly separate from the hypoconid, and the paraconid is formed as a broader, flatter lophid.

Talpavus nitidus Marsh, 1872
(Fig. 9; Table 6)

REFERRED SPECIMENS: YPM 16334, LP_4-M_2; CM 13717, LP_4-M_2; AMNH 11488, $LM_{2\text{-}3}$; AMNH 55686, RM_3.

LOCALITIES: Dry Creek, Henry's Fork, and locality 5, Bridger Formation (Upper), Wyoming; Powder Wash, Green River Formation, Utah.

KNOWN DISTRIBUTION: Bridgerian, Wyoming, Utah.

REMARKS: I concur with Robinson's (1968b) description of *T. nitidus*, which was based on the type and YPM 16334. The latter specimen and the other material referred here resemble the type, and differ from *S. priscus* in those features noted above: the paraconid on M_2 is thinner, more blade-like, the talonid is as wide as the trigonid, and the hypoconulid is smaller and not as clearly separated from the hypoconid. Apart from the structure of M_2, examination of the referred material of *T. nitidus* discloses additional diagnostic criteria, especially a narrow, premolariform P_4 with an unbasined talonid. Significantly, the talonid of P_4 also lacks cusps—a major distinction between *T. nitidus* and other material ascribed below to *Talpavus*. The structure of P_4, the paraconid on M_1, and the triangular, uncompressed trigonid on M_1 also distinguish *T. nitidus* from *S. priscus*. In *S. priscus*, P_4 is wider, the talonid is basined, the metaconid is less well developed, the trigonid on M_1 is more nearly square in occlusal outline, and the M_1 paraconid is a stronger lophid, more nearly vertical, and closer to the metaconid.

Talpavus cf. *T. nitidus*
(Fig. 10; Table 6)

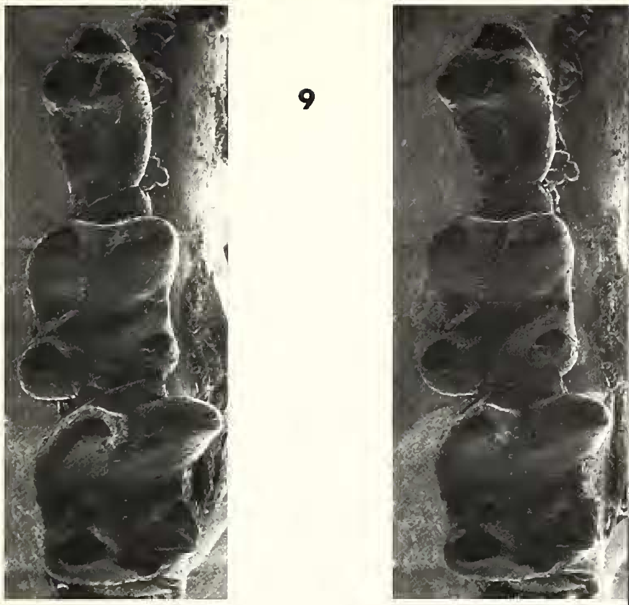
REFERRED SPECIMENS: CM 12122, LP_4-M_3; CM 13715, $RP_{3\text{-}4}$; CM 13716, LP_4-M_1; CM 13718, $RP_{3\text{-}4}$, CM 13754, RM_1; CM 26087, LP_3-M_1; CM 26260, $LM_{1\text{-}3}$; CM 26261, $RM_{1\text{-}2}$; CM 31180, LP_3-M_3; CM 31181, RM_3; CM 26267, RP_4-M_3; AMNH 55226, LP_4-M_3.

LOCALITIES: Greybull horizon, Willwood Formation, Big Horn Basin, Wyoming; Powder Wash, Green River Formation, Utah; Huerfano Formation, Colorado.

KNOWN DISTRIBUTION: Early Wasatchian, Wyoming; early Bridgerian, Utah; late Wasatchian, Colorado.

Fig. 9. *Talpavus nitidus*, CM 13717, RP_4-M_2, Green River Formation, Utah, approx. X 20. Fig. 10. *Talpavus* cf. *T. nitidus*. (A) CM 12122, LP_4-M_3, and (B) CM 26260, $LM_{1\text{-}3}$, Willwood Formation, Wyoming, approx. X 12; (C) CM 26087, LP_3-M_1, Green River Formation, Utah, approx. X 12. Fig. 11. *Talpavus duplus*, new species. Type, CM 12061, LP_4-M_3, Uinta Formation, Utah, approx. X 12.

▶



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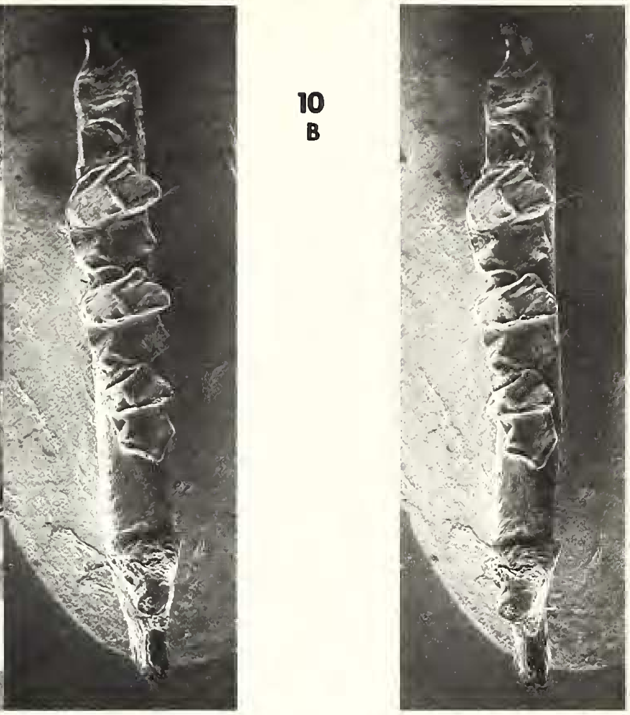

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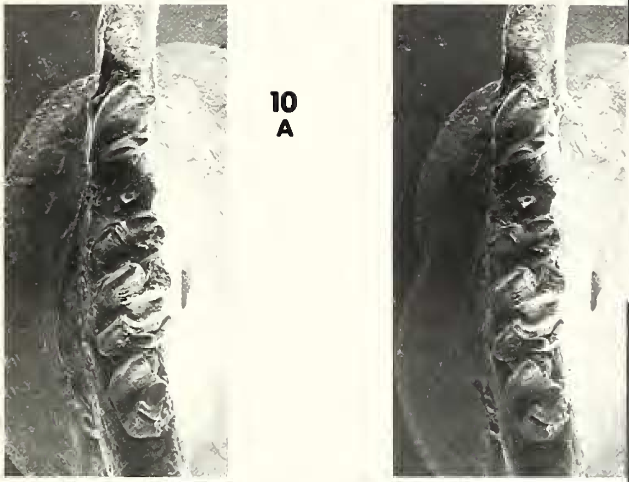

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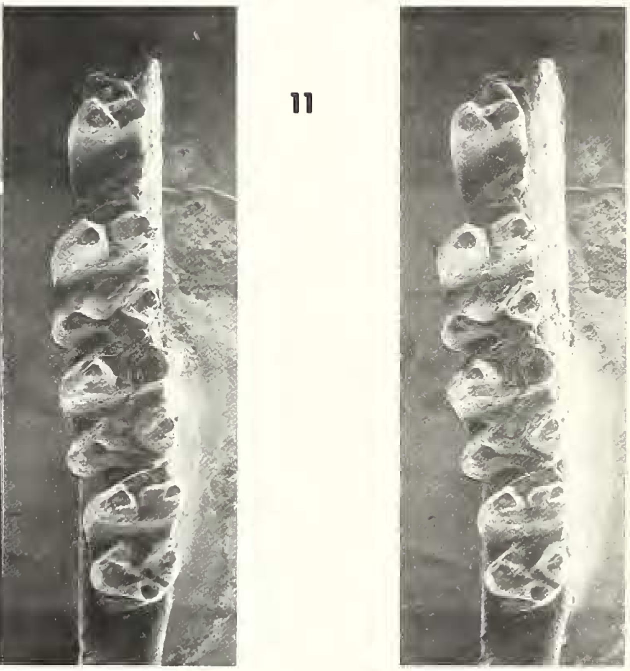

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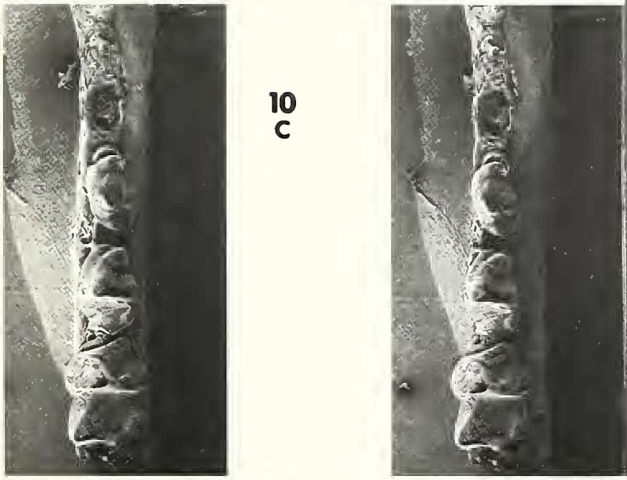


10
C

REMARKS: Only two features distinguish this material from *T. nitidus:* slightly smaller size and the occurrence of two cuspules (?entoconid and hypoconulid) on the raised posterior margin of the talonid of P_4. P_3, preserved on CM 13715, CM 13718, CM 26087, and CM 31180, is smaller than P_4, double-rooted, somewhat laterally compressed, and bears a small paraconid, a protoconid and a short talonid. As in *T. nitidus*, P_4 of cf. *T. nitidus* is narrow, and its talonid is short, unbasined, and lacks a cristid obliqua. The P_4 metaconid is almost as large and tall as the protoconid, and the paraconid is low, rounded, and well developed. The trigonid on M_1 is not compressed, but triangular in occlusal aspect, and the paraconid is blade-like and canted anterolingually, so that the trigonid is open lingually. The trigonid on M_2 is more compressed than on M_1, and is as wide as the talonid. The hypoconulid on M_{1-2} is slightly more separated from the hypoconid in comparison to the condition in *T. nitidus*, but is smaller than in *S. priscus*. The occurrence of cuspules on the talonid of P_4 may prove variable with recovery of additional *Talpavus* material. The structure of the known parts of the dentition of *Talpavus* implies that *Talpavus* had an origin in common with *Scenopagus*, especially *S. priscus*, from a *McKennatherium*-like adapisoricid, and differentiated with respect to the loss of the talonid basin on P_4.

AMNH 55226 from Huerfano was referred by Robinson (1966) to *Talpavus* cf. *T. nitidus*—an action recently questioned by Russell, et al. (1975) in their confusing analysis of *Talpavus*. Although wear on P_4 of AMNH 55226 has obliterated the details of the talonid structure, the latter appears to have been unbasined. Similarly, breakage and subsequent repair of the trigonids on M_{1-2} have produced artificially elongate molars. Nevertheless, as in *Talpavus*, the M_2 talonid is as wide as the trigonid, the hypoconulid on M_{1-2} is smaller than in *S. priscus* and is joined by a hypocristid to the hypoconid, P_4 is much narrower in relation to M_1 than is the case in *S. priscus*, and the paraconid on M_2 flares anterolingually.

Talpavus duplus, new species
(Fig. 11; Table 6)

TYPE: CM 12061, RP_4-M_3, and only known specimen.

TYPE LOCALITY: Myton pocket, Uinta Formation, Utah.

KNOWN DISTRIBUTION: Uintan of Utah.

ETYMOLOGY: *duplus*, L., double, referring to the double paraconid on P_4 and the close resemblance to *T. nitidus*.

DIAGNOSIS: Largest known species of *Talpavus*. Two cuspules form the paraconid on P_4.

DESCRIPTION AND REMARKS: The features that define *Talpavus* are well expressed on CM 12061. On P_4 the talonid is unbasined, but bears two cuspules in a fashion similar to P_4 of *Talpavus* cf. *T. nitidus*. The metaconid on P_4 is almost as large as the protoconid. The paraconid is formed as a ridge running anterolingually from the anterior face of the protoconid. Two cuspules occur on the ridge, one proximal to the protoconid and one forming the tip of the paraconid.

Apart from their larger size, M_{1-3} of *T. duplus* are similar to those of *T. nitidus* and cf. *T. nitidus*. The paraconid on M_1, although worn, appears to have been closer to the metaconid than in the latter species. However, features of *T. duplus* that are typical of *Talpavus* are the uncompressed trigonid on M_1, M_2 talonid and trigonid of equal width, and the small hypoconulid joined to the hypoconid by a hypocristid on M_{1-2}. *T. duplus* appears to be a Uintan representative of the same lineage that gave rise to the Wasatchian-Bridgerian species of *Talpavus*.

Adapisoricidae: Summary

The five genera, *McKennatherium*, *Scenopagus*, *Ankylodon*, *Macrocranion*, and *Talpavus*, seem to comprise a clade of lipotyphlans distinct from other early Tertiary Erinaceomorpha and Soricomorpha. The major trends in the origin and radiation of Paleocene and Eocene Adapisoricidae appear to be premolarization of the fourth premolar and the development of more nearly rectangular molars with lower, more bunodont cusps—trends shared with early erinaceids and many other early Tertiary mammals. In general, these are adaptations that emphasize crushing rather than puncturing and shearing during mastication. Specifically, P_4 in adapisoricids is primitively semimolariform, but becomes premolariform in Eocene species. M_{1-3} are characterized by a compressed, lophid-like paraconid that never joins the metaconid. The protoconid and metaconid are low, conical, almost bulbous cusps. The talonid is wide, moderately basined, and bears a high entoconid and a lower hypoconid that flattens with wear. The hypoconulid is median or barely lingual in position, and is not reduced. The hypoflexid notch is shallow; i. e., the cristid obliqua meets the trigonid below and labial to the notch between the protoconid and metaconid. Labial, lingual, or posterior cingulids are not developed.

The cusps on the upper molars are relatively low and conical. The stylar shelf is very narrow, without stylar cusps, and the hypocone and conules are well developed. In occlusal view, M^{1-3} are essentially rectangular and somewhat or moderately transverse. P^4, as yet unknown in Paleocene species, is premolariform in Eocene adapisoricids.

North American Paleocene adapisoricids are represented by *McKennatherium ladae* and a larger, contemporaneous species from the Rock Bench Quarries, Polecat Bench Formation. The Eocene genus *Scenopagus*, including *S. edenensis*, *S. curtidens*, and *S. priscus*, seems descended from *McKennatherium*, and ancestral to the late Eocene and Oligocene *Ankylodon*, the youngest known genus of the Adapisoricidae. *Talpavus*, represented by at least two species during the Eocene, has lost the talonid basin on P_4. *Macrocranion* may have had a European origin, but one species, *M. nitens*, occurs in early Eocene deposits of western North America. There is ample evidence that extensive faunal interchange occurred between North America and Europe during the Paleocene and early Eocene across a North Atlantic land corridor (Savage, 1971; Szalay and McKenna, 1971; McKenna, 1971, 1972a, 1972b; Dawson, et al., in press).

The bulk of recent work concerning early Tertiary lipotyphlans alludes to an ancestral-descendant relationship between adapisoricids and erinaceids, an inference that may have seemed possible if the Adapisoricidae were defined in a wastebasket sense (Van Valen, 1967, for example). As here understood, however, the two groups, by mid-Paleocene time, had differentiated to an extent that implies a considerable period of independent evolution prior to their earliest known (and contemporaneous) occurrence. Knowledge of their ancestry is clouded and will probably remain so until the record of North American Cretaceous eutherians improves, and until a number of early Paleocene faunas, which are currently under investigation, are described. Clemens (1973) has examined and tentatively refuted the possible relationships between *McKennatherium* and the late Cretaceous leptictid *Gypsonictops*. It also seems unlikely that adapisoricids originated from Late Cretaceous palaeoryctids, e. g., *Cimolestes*, *Procerberus*, or *Batodon*, for reasons similar to those stated by Clemens (1974) concerning the ancestry of the paromomyid primate *Purgatorius*. Palaeorictid lower dentitions are characterized by tall

Table 6. Dimensions of lower teeth of *Talpavus nitidus*, *Talpavus* cf. *T. nitidus*, and *T. duplus*, new species

	P_4		M_1			M_2			M_3		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
T. nitidus											
YPM 13511			—	—	1.2	1.6	1.1	1.1			
CM 13717	1.1	0.8	1.4	1.1	1.1	1.4	1.2	—			
AMNH 11488						1.4	1.2	1.2	1.3	1.0	0.8
Talpavus cf. *T. nitidus*											
CM 12122	1.1	0.7	—	—	—	1.2	—	1.0	1.1	—	—
CM 13715	1.2	0.8									
CM 13716	1.2	0.7	1.4	—	1.1						
CM 13718	1.1	0.8									
CM 13754			1.5	1.0	1.1						
CM 26087	1.1	0.7	1.4	1.0	1.0						
CM 26260			1.3	1.1	1.0	1.1	1.0	1.0	1.2	0.9	0.6
CM 26261			—	1.1	1.2	1.2	1.1	1.1			
CM 31180	1.1	0.8	1.3	1.0	1.0	1.1	1.0	1.0	1.2	0.9	0.7
CM 31181									1.2	0.9	0.8
CM 26267	1.0	0.7	1.4	1.1	1.0	1.2	0.9	0.9	1.2	0.9	0.7
AMNH 55226	1.2	0.8	1.4	1.1	1.1	1.4	1.1	1.1	1.4	1.0	0.7
Mean	1.12	0.75	1.38	1.05	1.06	1.20	1.02	1.02	1.24	0.92	0.70
T. duplus											
CM 12061 Type	1.4	0.9	1.6	1.1	1.2	1.6	1.2	1.2	1.6	1.1	1.0

trigonids and high, sharp cristids and cusps. Their upper molars are very transverse and lack hypocones or posterior cingula—features contrary to the more bunodont dental adaptations of adapisoricids. Some of the material of *Purgatorius* from the Puercan Garbani Locality, Montana, is, according to Clemens (1974), of definite insectivoran aspect, and in my view, especially like *McKennatherium*. The late Cretaceous erinaceotan from Alberta (Fox, 1970) seems to be a representative of a non-paleoryctid—leptictid group of insectivores that may have been ancestral to adapisoricids—a suggestion that Clemens (1974) also makes with reference to the ancestry of *Purgatorius*. In terms of dental morphology, the same Cretaceous stock that gave rise to adapisoricids (and other Lipotyphla) was probably also basal to the radiation of primates, dermopterans, bats, and tupaiids (the Archonta of Gregory, 1910, minus macroscelidids) as well as ungulates (McKenna, 1975).

Family Erinaceidae Fischer Von Waldheim, 1817

Many of the known early Tertiary insectivores have at one time or another been referred to this family. Simpson's (1945) Erinaceidae included *Entomolestes*, *Proterixoides*, *Metacodon*, and *Ankylodon*. Subsequently, *Scenopagus*, *Centetodon*, and *Talpavus* were also placed here (McKenna and Simpson, 1959; McKenna et al., 1962; Robinson, 1966). Van Valen (1967) limited the Erinaceidae to undoubted post-Eocene forms and relegated the above genera to the Adapisoricidae. These are now more strictly defined in this and other studies.

The early Tertiary North American Erinaceidae, as here understood, includes *Litolestes*, *Leipsanolestes*, possibly *Entomolestes grangeri*, and an unpublished form from the late Eocene of Wyoming (Setoguchi, M. S. thesis; McKenna, personal commun., 1974). Their shared-derived characters include a premolariform P_4, rectangular molars that progressively decrease in size from M_{1-3}, a dorsally flattened but cuspate paraconid on M_{2-3}, a greatly reduced hypoconulid, and a V-shaped talonid basin.

I agree with Butler (personal commun., 1975) and Russell (1964) that the European Paleocene *Adapisorex* is an erinaceid rather than an adapisoricid.

Litolestes Jepsen, 1930

L. ignotus, from the late Tiffanian of Wyoming, was described by Jepsen (1930) from partial remains of the lower dentition, and was referred, with question, to the Insectivora. In subsequent descriptions of two additional species, *L. notissimus* (Simpson, 1936) from Scarritt Quarry and *L. lacunatus* (Gazin, 1956) from Bison Basin, *Litolestes* was identified as a hyopsodontid condylarth. Van Valen (1967) however, returned *Litolestes* to the Insectivora as a creotarsine adapisoricid.

Although *Litolestes* is here described as an erinaceid, the affinities of *L. notissimus* and *L. lacunatus* are not as clear. As discussed below, they do not resemble typical hyopsodontids. Rather, they may represent late Paleocene echinosoricine-like erinaceids.

Litolestes ignotus Jepsen, 1930
(Fig. 12; Table 7)

TYPE: PU 13362, RP_4-M_3, Polecat Bench Formation, Wyoming.

REFERRED SPECIMENS: PU 13354, LP_4-M_2; PU 13974, RP_4-M_3; PU 14064, RP_3-M_2 erupting; PU 19362, LP_3-M_3; PU 19387, LP_2-M_2.

LOCALITY: Silver Coulee Quarries, Polecat Bench Formation, Wyoming.

KNOWN DISTRIBUTION: Late Tiffanian, Wyoming.

DESCRIPTION AND REMARKS: The lower antemolar dentition of *L. ignotus* has been dealt with elsewhere (Schwartz and Krishtalka, 1976) and need not be redescribed in detail. I_{2-3} of *L. ignotus* are comb-like with digitate, trilobed crowns. The crowns on lower incisors of later Tertiary and Recent erinaceids are not divided, but spatulate. However, incisors with divided crowns are not characters that imply phyletic relationships, inasmuch as these have evolved independently in many groups of mammals including Dermoptera, Macroscelidea, Carnivora, Notoungulata, and a variety of living and extinct insectivores (cf. Rose, 1973).

The fourth tooth in the jaw, traditionally identified as the canine in *L. ignotus*, is small, single-rooted, and fully premolariform. On this and other bases, Schwartz and Krishtalka (1976) concluded that this tooth may represent the first of five lower premolars in *L. ignotus* (and in the dermopteran *Plagiomene multicuspis*). As noted previously concerning *Ankylodon*, in addition to identifying this tooth as a premolariform canine or a premolar, a third interpretation—a deciduous canine—is possible, since the alleged dC_1 in another insectivore, *Nesophontes*, is also small, single-rooted, and premolariform. However, the homology of that locus in *Nesophontes* is uncertain, since both "dC_1" and "C_1" are premolariform and perhaps represent a deciduous premolar and its permanent successor, respectively. Accordingly, the tooth immediately posterior to I_3 in *L. ignotus* (and *Plagiomene*) is here tentatively identified as dP_1, a premolariform deciduous premolar that is retained in an antemolar dental complement of $I_1I_2I_3dP_1P_2P_3P_4P_5$. However, in the following portion of this paper, the standard post-incisor nomenclature of C_1P_{1-4} is employed for reasons outlined in the introduction and to facilitate comparisons of canine and premolar morphologies.

P_4 is premolariform and as large as M_1, as in typical early erinaceomorphs. The protoconid is dominant, the paraconid is small and anterolingual, and the metaconid is low on the posterolingual slope of the protoconid. The talonid is short, as wide as or wider than the trigonid, and the talonid basin is lingual and very narrow—approximately one-fourth or one-fifth of the width of the talonid. A tiny cuspule occurs at the posterior tip of the cristid obliqua. The labial portion of the talonid slopes ventrolabially away from the cristid obliqua.

The molars decrease markedly in size from M_1 to M_3. The protoconid and metaconid are low and conical. Significantly, the paraconid on M_1 is slightly compressed, but is more nearly erect and cuspate than on M_{2-3}. On the latter, the paraconid is more nearly medial and flattened so that it projects anteriorly. The talonid is as long and wide as the trigonid on M_{1-2}, but is elongate on M_3 because of a posteriorly projecting hypoconulid. The entoconid is higher than the hypoconid, but neither cusp is formed as a distinct cone. Rather, they are elongate anteroposteriorly, with flat internal walls that slope ventromedially so that the talonid basin is not rounded, but a V-shaped valley. The internal walls of both cusps extend to the trigonid and close the talonid basin lingually and labially. The bottom of the talonid valley is formed as a midline, which runs from the trigonid to the posterior margin of the talonid. On M_{1-2} the hypoconulid is extremely reduced and occurs on the posterior edge of the entoconid wall, just lingual to the midline. The posterior edge of the talonid is nearly straight.

These features of *L. ignotus* are equally diagnostic of undoubted later Tertiary erinaceids and, most especially, a new mid- or late-Eocene species from the Tepee Trail Formation, Wyoming, currently being described by McKenna (personal commun., 1974). *L. ignotus* seems slightly more primitive than the latter in lacking posterior cingulids on the lower molars, in possessing higher protoconids on P_{2-3}, and a slightly more developed talonid on P_4.

In contrast to *L. ignotus*, the lower canine in *L. notissimus* and *L. lacunatus* is large and recurved, P_2 and P_3 are more elongate and bear a small low paraconid, the talonid on P_4 is relatively longer and wider, and the metaconid and protoconid on M_{1-3} are slightly more bulbous. The hypoconulid is not reduced on M_{1-3} of *L. notissimus* and *L. lacunatus*, the talonid basin is more nearly rounded than V-shaped, and the cristid obliqua is oriented less nearly parallel to the entocristid, compared to that of *L. ignotus*.

Russell, et al. (1975), alluded to the condylarthran nature of *Litolestes*, although they retained that genus in the Adapisoricidae. One of the problems of their review is the failure to discuss the genotype, *L. ignotus*. Only *L. notissimus* was considered. That species, as well as *L. lacunatus*, superficially resemble hyoposodontids, mainly in the semibulbous nature of the molar protoconids and metaconids, compared to those of *L. ignotus*. However, in hyoposodontids known to me the molars are considerably more robust and less angular in occlusal outline. M_2 is invariably larger than M_1 and M_3, the molar paraconids are reduced to a simple ridge between the protoconid and metaconid, and P_4 is semimolariform or submolariform. As in *L. ignotus* and the Tepee Trail erinaceid, the lower molars of *L. notissimus* and *L. lacunatus* are not robust, they decrease progressively in size from M_1 to M_3, the paraconid on M_1 is slightly compressed but is not reduced, and the paraconids on M_{2-3} are dorsally flattened but cuspate.

L. notissimus and *L. lacunatus* are stratigraphically older than *L. ignotus*. As erinaceids, they have more plesiomorphic features than *L. ignotus*, e.g., the unreduced hypoconulid and a more nearly rounded talonid basin on the lower molars, and a slightly longer talonid on P_4. Of interest is the large lower canine of *L. notissimus* and *L. lacunatus*, a feature absent in *L. ignotus* (Schwartz and Krishtalka, 1976) and later erinaceines (Butler, 1948), but retained in many echinosoricines (Butler, 1948). *L. notissimus* and *L. lacunatus* may represent the early echinosoricine condition in which a canine and four premolars are derived from a *Kennalestes*-like dental complement of a canine and five premolars. *L. ignotus*, on the other hand, with loss of the lower canine and retention of five premolars, may mirror the origin of the erinaceine lower dentition.

The known parts of the upper dentition of *L. ignotus* and *L. notissimus* (AMNH 33942, 33944) are less erinaceid-like than those of the lower dentition. P^4 in these species lacks a metacone, and is premolariform. M^{1-3} are typically adapisoricid-like: molars wider than long and shorter lingually than labially, narrow stylar shelves, rectangular occlusal outline with a shallow labial emargination and a constriction across the conules, conical or subconical paracone and metacone, well-developed conules with internal wings, a hypocone, and a weak anterior cingulum—characters that are plesiomorphic for many Paleocene eutherians like primates, lipotyphlan insectivores, pantolestids, apatemyids, and condylarths, and not indicative of phylogenetic relationships among taxa within these groups.

With regard to adapisoricids, two of the derived characters of upper molars of early erinaceids are the progressive reduction in size from M^1 to M^3 and the posterolabial position of the hypocone relative to that of the protocone—characters that occur in the Tepee Trail erinaceid. In *Litolestes*, the hypocone on $M^{1\text{-}2}$ occurs more nearly posterior than posterolingual to the protocone. M^2 of *Litolestes* is not larger than M^1 to the degree seen in adapisoricids and hyopsodontids. Rather, M^2 is shorter than M^1, and is slightly wider only in the area of the stylar shelf. In these respects the upper dentition of *Litolestes* approaches the typical erinaceid condition but is primitive relative to the upper dentition of the erinaceid from Tepee Trail.

Leipsanolestes Simpson, 1928

This genus is known only from the lower dentition of one species. Simpson (1928) originally described *L. seigfriedti* as an adapisoricid, but later (1929) referred *Leipsanolestes* to a subgenus of *Leptacodon*. McKenna (1960a) argued for inclusion of *L. seigfriedti* in *Entomolestes*, whereas Robinson (1968b) placed the species in *Talpavus*. Russell, et al. (1975), provisionally retained *Leipsanolestes* as a valid genus in the Adapisoricidae.

As described below, the molar morphology of *Leipsanolestes* is very similar to that of *Litolestes ignotus*, and differs from *M. nitens* and *Talpavus*, especially in those features that distinguish early erinaceids from adapisoricids.

Leipsanolestes seigfriedti Simpson, 1928
(Fig. 13; Table 7)

TYPE: AMNH 22157, $RM_{2\text{-}3}$, Fort Union Formation, Montana.

REFERRED SPECIMENS: CM 11517, LP_4-M_1; CM 11519, RP_4-M_1; CM 11532, LM_1; CM 11553, RP_4-M_3; CM 11662, LP_4, M_2; CM 11664, LP_4; CM 11676, RM_1; CM 11704, R1/2M_1-M_2; AMNH 56317, $RM_{1\text{-}3}$.

LOCALITIES: Bear Creek, Fort Union Formation, Montana; Reclusa Blowout, Powder River local fauna, Wyoming.

KNOWN DISTRIBUTION: Late Tiffanian, Montana; early Wasatchian, Wyoming.

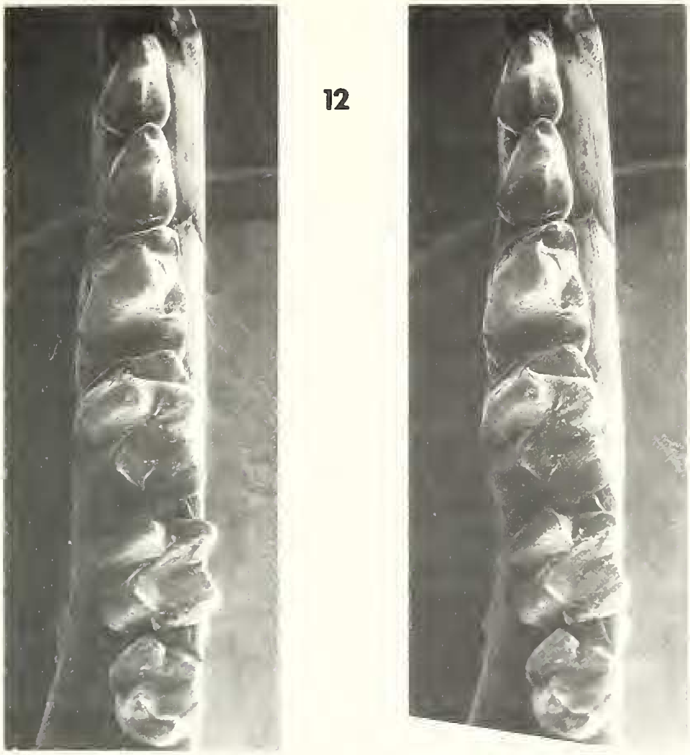
DESCRIPTION AND REMARKS: Teeth anterior to P_4 are unknown. P_4 is semimolariform, with the talonid almost as long as the trigonid. The paraconid is bulbous, anterolingual, and as large as the metaconid. The metaconid occurs slightly higher than the paraconid on the posterolingual face of the protoconid. The talonid bears two tiny cusps, an entoconid and hypoconid, which, respectively, form the posterior tips of the long and parallel entocristid and cristid obliqua. The talonid basin between these two cristids occupies approximately one-half the width of the talonid.

The molars of *Leipsanolestes seigfriedti* are low and rectangular, and decrease in size from M_1 to M_3, although not as radically as in *Litolestes ignotus*. The paraconid is fully cuspate and is flattened dorsally to produce a low angular shelf. The protoconid and metaconid are blunt, conical cusps, and the talonid basin is developed as a V-shaped valley. The internal walls of the entoconid and hypoconid are flat, oriented ventromedially toward the talonid basin, and extend anteriorly to meet the trigonid. The hypoconulid is extremely reduced on $M_{1\text{-}2}$, but is discernible on the posterior edge of the entoconid, just lingual to the midline. As a result, the posterior margin of the talonid on $M_{1\text{-}2}$ is nearly straight, as is the case in *L. ignotus*, *Entomolestes grangeri*, and the late Eocene erinaceid from Tepee Trail.

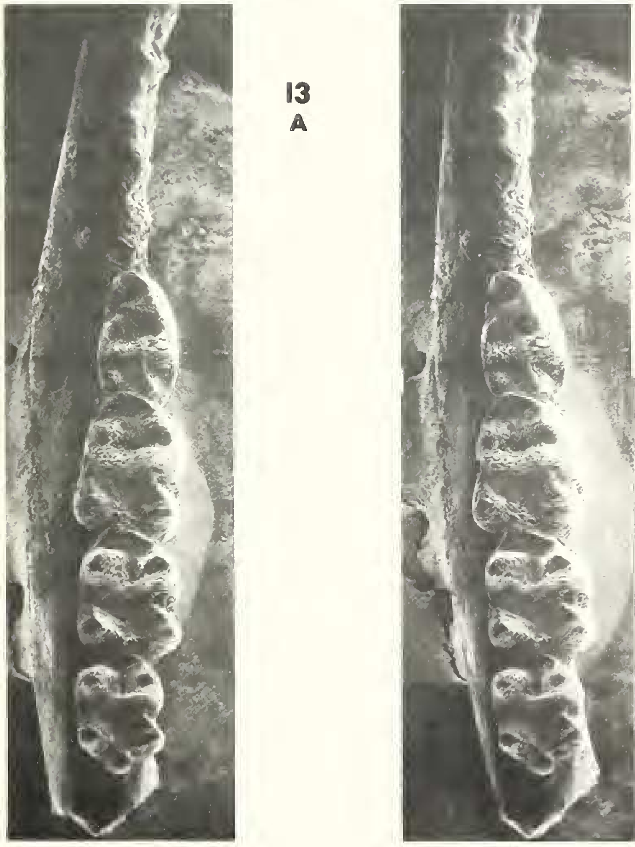
Although *Leipsanolestes seigfriedti* and *Litolestes ignotus* were contemporaneous erinaceids, the former is more primitive in the retention of a semimolariform P_4 and the less-marked reduction in size of the molars from M_1 to M_3. However, the structure of the molars of *L. seigfriedti* is unquestionably erinaceid-like. This species may represent an early lineage of erinaceids that, with *Litolestes*, shared an early Paleocene or older ancestry from a form with a semimolariform P_4.

Delson (1971) erroneously referred AMNH 56317, partial right mandible with $M_{1\text{-}3}$ from the early Eocene Powder River local fauna, to *Entomolestes* cf. *nitens*. The molars are virtually identical to those of *L. seigfriedti* except for the complete loss of the hypoconulid on the Eocene form. This specimen is here

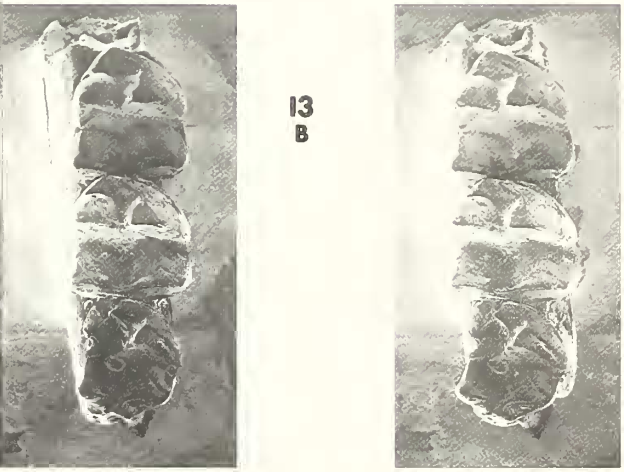
Fig. 12. *Litolestes ignotus*, PU 19387, Polecat Bench Formation, Wyoming, approx. X 12. Fig. 13. *Leipsanolestes seigfriedti*. (A) CM ▶ 11553, RP_4-M_3, Fort Union Formation, Montana; (B) AMNH 56317, $RM_{1\text{-}3}$, Wasatch Formation, Wyoming; both approx. X 12.



12



13 A



13 B

assigned to *L. seigfriedti*, although recovery of additional material may determine that AMNH 56317 warrants specific distinction from *L. seigfriedti*.

The confusion concerning the affinities of *Leipsanolestes* was not resolved in the recent discussion by Russell, et al. (1975). The authors compared this genus only to "*Entomolestes*" *nitens*, noted a number of diagnostic differences and concluded that the two species shared a special affinity among adapisoricids.

In comparison to *Macrocranion nitens*, P_4 of *Leipsanolestes* is semimolariform rather than premolariform. The talonid is more elongate and the talonid basin occupies one-half the width of the talonid. M_{1}-$_{3}$ of *Leipsanolestes* (and other erinaceids) are distinct from those of *M. nitens* (and other adapisoricids) in that they are more rectangular in occlusal outline and show a progressive reduction in size. The talonid on M_{1}-$_{2}$ of *Leipsanolestes* is not longer than the trigonid, the hypoconulid is extremely reduced, the talonid cusps occur posteriorly along the nearly straight posterior margin of the talonid, and the paraconid is a low, fully cuspate, dorsally flattened shelf rather than a compressed lophid. *Scenopagus* and *Talpavus* differ from *Leipsanolestes* in the structure of P_4, and in possessing higher, sharper, molar cusps, and a deeper hypoflexid notch.

As discussed below, among species previously classified by most authors as adapisoricids, *Entomolestes grangeri* bears the closest resemblance to *Leipsanolestes*.

?Erinaceidae
Entomolestes Matthew, 1909
Entomolestes grangeri Matthew, 1909

The taxonomic history of this genus was discussed in an earlier section. The genotype, *E. grangeri*, is known only from the holotype, AMNH 11485, partial left mandible with P_3-M_3, from the upper part of the Bridger Formation, Middle Eocene of Wyoming. Apart from Robinson (1968b), previous considerations of *Entomolestes* failed to distinguish between *E. grangeri* and "*E.*" *nitens*, which I have referred above to *Macrocranion*.

Unfortunately, the molars on AMNH 11485 are damaged, obscuring potentially diagnostic features. However, the lower dentition bears a number of discernible erinaceid characters. Five alveoli are preserved anterior to P_3, and are interpreted by Robinson (1968b) to have been filled with I_{2}-$_{3}$, C_1, P_{1}-$_{2}$, all single-rooted. Robinson also noted, however, that the alveolus for P_2 is elongate and slightly hourglass-shaped, so that P_2 may have had two roots, as in other erinaceids. P_3 is double-rooted and has a low, blade-like, procumbent crown. P_4 is typically premolariform with an extremely short talonid and a single cuspule at the posterior tip of the cristid obliqua. The molars are low, rectangular in occlusal view, and lean anterolingually. M_3 is reduced, compared to M_{1}-$_{2}$, which are of equal size. The talonids are as wide as the trigonids and not elongate, whereas the opposite is true in *M. nitens*. The paraconid, damaged on M_1 and M_3, is low, somewhat compressed, and oriented anterolingually on M_2. The metaconid and protoconid are quite worn, but appear to have been well developed and conical. The hypoflexid notch is shallow, as in other erinaceomorphs, since the cristid obliqua originates labially on the posterior wall of the trigonid. The entoconid is high, elongated anteroposteriorly, and has a flat internal wall that slopes ventromedially to the bottom of the talonid basin. A tiny notch occurs lingually at the junction of the high entocristid and the posterolingual face of the metaconid. The hypoconid is worn flat. The hypoconulid on M_{1}-$_{2}$ is reduced and occurs on the posterior edge of the entoconid, just lingual to the midline, as is also the case in *L. ignotus* and *Leipsanolestes*. As a result, the talonid cusps are lined up along the nearly straight posterior margin of the talonid.

These characters imply the erinaceid affinities of *E. grangeri*. Although M_1 and M_2 are equal in size, the molars of *E. grangeri* most closely resemble those of *Leipsanolestes*. Clearly, more complete *E. grangeri* material is needed before its relationships can be accurately assessed.

Erinaceidae: Summary

The two or possibly three known genera that comprise the North American early Tertiary record of erinaceids can be readily distinguished from adapisoricids and soricomorphs on the basis of dental remains. P_{2}-$_{4}$ are double-rooted, and P_4 is premolariform. The molars are rectangular in occlusal outline and decrease in size from M_1 to M_3. The paraconid, more nearly erect and lingual on M_1, is flattened dorsally into a shelf-like cusp on M_{2}-$_{3}$ and occurs closer to the midline. The protoconid and metaconid are low, conical cusps. The talonid basin is formed as a V-shaped valley by the flat internal walls of the hypoconid and entoconid. These cusps are also elongated anteriorly to the trigonid. The hypoconulid is extremely reduced on M_{1}-$_{2}$ and the hypoflexid notch is shallow.

In the earliest known erinaceid, *Litolestes*, some of these characters, like the structure of the talonid and the reduced hypoconulid, are less well expressed and imply the primitive condition. *Litolestes* and *Leipsanolestes* seem to represent two early, divergent lineages of erinaceids. Species of the former seem suitable morphologically and temporally to be representatives of early erinaceine and echinosoricine erinaceids. *L. ignotus* may be close to the ancestry of the late Eocene erinaceid from Tepee Trail, Wyoming.

Table 7. Dimensions of lower teeth of *Litolestes ignotus* and *Leipsanolestes seigfriedti*

	P_4		M_1			M_2			M_3		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
L. ignotus											
PU 13354	1.5	1.2	1.6	1.2	1.3	1.4	1.2	—			
PU 13974	1.7	1.2	1.7	1.3	1.3	1.5	1.3	1.3	1.3	1.0	0.9
PU 14064	1.6	1.2	1.7	1.2	1.2	1.5	1.2	1.2			
PU 14333	1.7	1.4	1.7	1.5	1.5						
PU 19362	1.7	1.4	1.8	1.5	1.5	1.5	1.3	1.3	1.4	1.2	1.0
PU 19387	1.8	1.3	1.8	1.4	1.4	1.6	1.4	1.3	1.4	1.0	0.9
Mean	1.67	1.28	1.72	1.35	1.36	1.48	1.28	1.28	1.37	1.07	0.93
L. seigfriedti											
CM 11517	1.5	1.0	1.8	1.4	1.5						
CM 11519	1.7	1.1	1.8	1.3	—						
CM 11532			1.6	1.4	1.4						
CM 11662	1.6	1.3				1.5	1.3	1.3			
CM 11676			1.8	1.3							
CM 11704			—	—	1.5	1.6	1.4	1.4			
AMNH 56317			1.7	1.2	1.3	1.6	1.3	1.4	1.4	—	1.1
Mean	1.60	1.13	1.74	1.32	1.42	1.57	1.33	1.37			

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Appendix A. Dimensions of lower teeth of *Scenopagus edenensis*, *S. curtidens* and *S. priscus*

	P_4		M_1			M_2			M_3		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
S. edenensis											
YPM 13612									2.5	1.8	1.4
YPM 14932						2.6	1.9	1.9			
YPM 14934			2.3	—	1.9	2.5	2.0	1.8			
YPM 16910						2.7	2.2	2.0	2.7	—	—
AMNH 11428			2.1	1.7	1.8	2.2	2.0	1.9			
CM 13739	2.0	1.6	—	1.9	—						
CM 13732						2.2	2.0	1.8	2.3	1.7	1.3
CM 13734	2.0	1.4	—	—	—						
CM 13728						2.2	—	—	2.3	1.7	1.4
CM 6444	2.1	1.5	2.3	1.9	—						
CM 6449			2.1	1.7	1.7	2.1	1.9	1.8	2.4	1.8	1.5
CM 13731			2.3	1.7	1.7						
CM 13740						2.3	2.0	1.8			
CM 6441	2.0	1.5				2.3	2.0	1.9			
CM 17318	2.2	1.5	2.4	1.9	2.0						
CM 13737	2.0	1.5									
CM 13730	2.0	—	2.1	—	—	2.1	—	—			
CM 13729			—	—	1.9	2.2	1.9	1.8			
CM 13735	2.0	1.4									
CM 6485	2.2	1.4	—	1.8	—						
CM 13733						2.2	2.1	1.8			
CM 13736									2.4	1.7	1.4
CM 13738	2.1	1.5									
CM 6443						2.1	1.9	1.8	2.3	1.7	1.3
CM 17317						—	—	1.8	—	1.7	1.3
TTU-P-5571						2.0	—	—			
TTU-P-5572									2.3	—	—
TTU-P-7161			2.3	1.7	1.8						
TTU-P-7162			2.3	1.9	2.0						
TTU-P-7163			2.1	1.8	1.7						
TTU-P-7164			2.3	1.8	1.9						
TTU-P-7165			2.1	1.7	1.7						
TTU-P-7166			2.3	1.9	1.9						
TTU-P-7180						2.2	2.0	1.9			
TTU-P-7181						2.1	1.8	—			
TTU-P-7182						2.3	1.9	1.8			
TTU-P-7183						2.3	1.9	1.8			
TTU-P-7184						2.2	1.9	1.8			
TTU-P-7185						2.3	2.0	1.9			
TTU-P-7186						2.3	1.9	1.8			
TTU-P-7187						2.2	2.0	1.9			
TTU-P-7188									2.4	1.7	1.2
TTU-P-7189									2.2	1.7	1.3
S. curtidens											
YPM 16913			1.8	1.6	1.6	1.8	1.6	1.4			
YPM 14939			1.9	1.5	1.5	1.8	1.6	1.5			
YPM 13610-1A	1.5	1.1									
YPM 13610-1B	1.5	1.2	1.8	1.5	1.6	1.8	1.6	1.5			
YPM 13610-2			1.7	1.4	1.5	1.7	1.5	1.4			
YPM 15255						1.8	—	1.4	1.6	1.2	0.9
YPM 15254	1.5	1.2	1.8	1.5	1.6	1.8	1.6	1.5	1.6	1.2	1.1
YPM 16912	1.5	1.2	1.7	1.6	1.5						
AMNH 12058						1.8	1.6	1.5	1.6	1.3	1.2
AMNH 12055			—	—	1.5	1.8	1.7	1.5	—	1.3	—

Appendix A. Dimensions of lower teeth of *Scenopagus edenensis*, *S. curtidens* and *S. priscus*, continued

	P_4		M_1			M_2			M_3		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
S. curtidens											
AMNH 12062			—	—	1.5	1.7	1.6	1.4	—	1.2	—
AMNH 12064	1.5	1.2	1.8	1.5	1.5						
AMNH 11491			2.0	1.5	1.5						
AMNH 48183	1.6	1.2				1.9	1.5	1.6			
AMNH 59643			2.0	1.5	1.6						
UCMP 96155			1.7	1.4	1.5	1.7	1.5	1.4	1.7	1.3	1.0
TTU-P-3928			—	—	1.6	1.7	1.6	1.5	1.5	1.3	1.0
TTU-P-7054			1.8	1.4	1.5						
S. priscus											
AMNH 56060			1.4	1.1	1.2	1.5	1.3	1.2	1.3	0.9	—
AMNH 55156	1.3	1.0	1.5	1.3	1.3						
CM 13753	1.3	1.0	1.5	1.2	1.2						
CM 13749			1.5	1.2	1.2	1.4	1.3	1.1			
CM 13750	1.3	0.9	1.5	1.2	1.3						
CM 13744	—	1.1									
CM 17316						1.4	1.3	1.1	—	1.1	—
CM 13746			1.5	1.1	1.1						
CM 13743						1.5	—	—	1.3	0.9	0.8
CM 13748			1.5	1.1	1.1	1.5	1.5	1.1	1.0		
CM 6486	1.2	0.9	1.5	1.1	1.2	1.4	1.2	1.0			
CM 17319						1.5	1.2	1.0	1.3	1.0	0.7
CM 13751	1.3	0.9	1.4	1.3	1.3	1.4	1.3	1.1			
CM 13752	1.4	0.9	1.5	1.1	1.3						
TTU-P-7094			1.4	1.0	1.2						
TTU-P-7098			1.3	0.9	1.0						
TTU-P-7099			1.4	1.1	1.2						
TTU-P-7097			1.4	1.0	1.1						
TTU-P-7096			1.3	0.8	0.9						
TTU-P-7100			1.3	0.9	1.0						
TTU-P-7082			1.4	0.9	1.0						
TTU-P-7092			1.5	1.0	1.1						
TTU-P-7093			1.3	0.9	—						
TTU-P-7081			1.4	0.9	—						
TTU-P-7083			1.4	0.9	1.0						
TTU-P-7084			1.5	1.1	1.1						
TTU-P-7085			1.5	1.0	1.1						
TTU-P-7090			1.4	1.0	1.0						
TTU-P-7095			1.4	1.0	1.0						
TTU-P-7087			1.5	1.0	1.1						
TTU-P-7086			1.5	1.0	1.1						
TTU-P-7088			1.4	1.0	1.1						
TTU-P-7120			1.4	0.9	1.0						
TTU-P-7121			1.4	1.0	1.0						
TTU-P-7119			1.5	1.1	1.0						
TTU-P-7124						1.5	1.2	1.0			
TTU-P-7125						1.4	1.1	0.8			
TTU-P-7117						1.6	1.2	0.9			
TTU-P-7118						1.5	1.2	1.0			
TTU-P-7089						1.4	1.2	1.1			
TTU-P-7122						1.4	1.2	1.1			
TTU-P-7129						—	—	—			
TTU-P-7131						1.4	1.1	1.0			
TTU-P-7132						1.5	1.3	1.1			

Appendix A. Dimensions of lower teeth of *Scenopagus edenensis, S. curtidens* and *S. priscus,* continued

	P_4			M_1			M_2			M_3	
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
S. priscus											
TTU-P-7130						1.4	1.1	1.0			
TTU-P-7126						1.4	1.2	1.1			
TTU-P-7127						—	1.1	—			
TTU-P-7128									1.3	0.9	0.7
TTU-P-7123									1.4	0.9	0.7
TTU-P-7140									1.5	1.0	0.8
TTU-P-7137									1.4	0.9	0.7
TTU-P-7138									1.3	1.0	—
TTU-P-7139									1.3	0.8	0.6
TTU-P-7135									1.3	0.9	0.7
TTU-P-7142									1.4	1.0	0.7
TTU-P-7134									1.3	—	—
TTU-P-7141									1.3	1.0	0.7
TTU-P-7143									1.3	1.1	0.8
TTU-P-7136									1.3	0.9	0.7

Appendix B. Dimensions of upper teeth of *Scenopagus edenensis* and *S. priscus*

	P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W
S. edenensis								
YPM 16911			2.3	3.3				
CM 6433	——	2.6	2.3	3.1	2.2	3.5		
CM 13741	2.0	2.6	2.2	3.2	2.0	3.4		
TTU-P-7145	2.0	2.8						
TTU-P-7146	2.0	2.9						
TTU-P-7147	2.0	2.6						
TTU-P-7148	2.0	2.7						
TTU-P-7149	2.0	2.6						
TTU-P-7150			2.2	3.2				
TTU-P-7155			2.3	3.3				
TTU-P-7156			2.4	3.2				
TTU-P-7152			——	3.3				
TTU-P-7160			——	——				
TTU-P-7159			2.1	3.2				
TTU-P-7153			——	3.1				
TTU-P-7175			——	3.1				
TTU-P-7151			2.2	3.0				
TTU-P-7167					2.1	——		
TTU-P-7169					2.1	3.1		
TTU-P-7178					——	3.3		
TTU-P-7168					——	3.4		
TTU-P-7172					2.1	3.2		
TTU-P-7179					2.1	3.3		
TTU-P-8232							1.9	2.8
TTU-P-8233							1.5	2.6
TTU-P-8234							1.6	2.8
S. priscus								
TTU-P-7051	1.4	2.0						
TTU-P-7060			1.4	2.0				
TTU-P-7075			1.5	2.1				
TTU-P-7074			——	2.0				
TTU-P-7062			1.5	2.0				
TTU-P-7077			1.4	2.1				
TTU-P-7080			1.6	2.1				
TTU-P-7076			1.4	2.0				
TTU-P-7059			1.4	1.9				
TTU-P-7057			1.5	2.1				
TTU-P-7053			1.5	2.1				
TTU-P-7068			1.6	2.2				
TTU-P-7065			1.5	2.1				
TTU-P-7056			——	2.1				
TTU-P-7071			1.4	2.0				
TTU-P-7079			——	2.1				
TTU-P-7072			1.5	2.1				
TTU-P-7070			1.4	2.0				
TTU-P-7063			1.5	——				
TTU-P-7102					——	2.0		
TTU-P-7116					1.4	1.9		
TTU-P-7112					1.3	2.2		
TTU-P-7109					1.1	2.0		
TTU-P-7115							1.3	2.2
TTU-P-7107							1.4	2.1
TTU-P-7113							1.4	2.2

Appendix C. Dimensions of lower teeth of *Macrocranion nitens* and *Macrocranion* cf. *M. nitens*

	P_4			M_1			M_2			M_3	
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
M. nitens											
AMNH 48172						1.8	----	1.6	1.9	1.3	1.3
AMNH 48174	2.0	1.3	2.1	1.5	1.6	2.1	1.6	1.6	2.2	1.4	1.4
AMNH 48176			1.9	1.5	1.5	1.9	1.5	1.6	----	----	1.4
AMNH 48178	1.7	1.2	1.9	1.4	1.5	2.0	1.4	1.6	2.0	1.2	1.3
AMNH 48179	1.6	1.1	1.9	----	1.5	2.0	1.4	1.5			
AMNH 48180	1.8	1.1	1.9	1.5	1.6	1.8	1.5	1.6			
AMNH 48182						2.0	1.5	1.6			
AMNH 48184			1.9	1.4	1.5	2.0	1.5	1.6			
AMNH 48187									2.0	1.2	1.3
AMNH 48189	1.7	1.2	1.9	1.4	1.5	2.0	1.5	1.6			
AMNH 15697	1.8	1.2	1.9	1.3	1.6	2.0	1.4	----			
AMNH 14674	----	1.3	2.1	1.4	1.6	2.0	1.6	1.7	2.2	1.4	----
Macrocranion cf. *M. nitens*											
AMNH 59673	----	----	1.6	1.3	1.5	1.7	1.4	1.5	1.7	1.2	1.3
AMNH 59662	1.4	0.9									
AMNH 59656						1.8	1.4	1.5	1.7	----	1.3
AMNH 59663	1.4	1.0									
AMNH 80071			1.8	1.4	1.5						
AMNH 59679	1.4	0.9	1.7	1.3	1.4						
AMNH 59651	1.4	0.9									
AMNH 59688	1.7	1.1									
AMNH 88846			1.8	1.4	1.5						
AMNH 88834			1.8	1.4	1.5						
AMNH 88839			1.8	1.3	1.4						
AMNH 88830			1.8	1.4	1.5	1.7	1.5	1.6			
AMNH 56318	1.5	1.0									